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RESTAURATION FORESTIÈRE DE TERRES AGRICOLES ABANDONNÉES : EFFETS DES INTERACTIONS BIOTIQUES SUR L'ÉTABLISSEMENT DES ARBRES

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ANNICK ST-DENIS

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La thèse est présentée sous la forme de trois articles scientifiques rédigés en anglais. J'ai été responsable des designs expérimentaux, de la collecte des données sur le terrain et en laboratoire, de la compilation et de l'analyse des données ainsi que de la rédaction. Christian Messier et Daniel Kneeshaw ont collaboré au design expérimental des trois chapitres alors que Dominic Senecal de WSP s'est impliqué sur les objectifs appliqués des deux premiers chapitres. Un stage de deux mois au laboratoire de Suzanne Simard de la Faculté de Foresterie de *University of British Columbia* (UBC) m'a aidé à élaborer les objectifs et la méthodologie du chapitre III.

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AC	Colonisation par les arbuscules, *Arbuscular colonization*
AM	Mycorhize arbusculaire (endomycorhizienne), *Arbuscular mycorrhizal*
ANOVA	Analyse de variance, *Analysis of variance*
ANOVAR	Analyse de variance à mesures répétées, *Repeated measures analysis of variance*
BS	Sol à nu, *Bare soil*
C	Carbone, *Carbon*
EM	Ectomycorhize (ectomycorhizienne), *Ectomycorrhizal*
HC	Colonisation par les hyphes, *Hyphae colonization*
JCH	Hypothèse de Janzen-Connell, *Janzen-Connell hypothesis*
M	Paillis, *Mulch mat*
N	Azote, *Nitrogen*
P	Phosphore, *Phosphorus*
RDA	Analyse de redondance, *Redundancy analysis*
RGR	Taux de croissance relative, *Relative growth rate*
SGH	Hypothèse du gradient de stress, *Stress-gradient hypothesis*
SWC	Contenu en eau du sol, *Soil water content*
VG	Végétation, *Vegetation*

RÉSUMÉ

Au courant des dernières décennies, de plus en plus de terres agricoles ont été abandonnées. Bien que les causes puissent être différentes, le phénomène est observé dans plusieurs régions du monde. Suite à l'abandon, la succession végétale mène parfois à une afforestation naturelle dominée par quelques espèces d'arbres anémochores. Dans d'autres cas, la végétation rudérale inhibe pendant de nombreuses années l'établissement ou la croissance des espèces forestières. Plusieurs projets de reboisement ont été instaurés avec une attention portée sur les relations de compétition et de prédation. Or, des relations de facilitation ou de tolérance peuvent aussi s'observer entre la végétation herbacée et les jeunes arbres plantés. Les relations entre les microorganismes du sol et les arbres vont quant à elles des effets pathogènes au mutualisme. Ces relations positives, neutres ou négatives sont influencées par les facteurs environnementaux comme l'humidité du sol et la disponibilité des nutriments du sol.

Notre projet avait pour but d'analyser les effets de plusieurs interactions biotiques sur l'établissement des arbres dans une optique de restauration forestière de terres agricoles abandonnées. Nous avons donc étudié les relations de compétition, mais aussi de facilitation et de tolérance entre les plantes herbacées et les arbres, la prédation des semences et des semis, ainsi que les effets des microbes de sol forestier sur les arbres.

Un premier dispositif expérimental en champ nous a permis d'évaluer les effets (positifs, neutres ou négatifs) de la végétation herbacée ainsi que les effets de la prédation sur la germination, la survie et la croissance de six espèces d'arbres indigènes. Nos hypothèses

étaient que les taux de germination et de survie augmenteraient avec la taille des semences et que la végétation herbacée aurait des effets positifs sur la germination de l'espèce tolérante à l'ombre, mais négatifs sur les espèces intolérantes à l'ombre. Les espèces ayant de petites semences ont peu ou pas germé, mis à part le pin rouge dont la survie après un an était très faible. Le chêne rouge, l'espèce ayant les plus larges semences, a eu les taux de germination et de survie les plus élevés. Aucune prédation n'a été observée et la végétation herbacée n'a eu aucun effet, mis à part des effets négatifs sur le diamètre des semis de chêne rouge. Nos résultats supportent les hypothèses que la taille des semences influence le succès de l'ensemencement en champ et que l'ensemencement peut se faire dans la végétation herbacée.

Un second dispositif expérimental a été utilisé afin d'évaluer les effets de la végétation herbacée et ceux de la prédation par les petits mammifères sur huit espèces d'arbres plantés. Les six espèces feuillues et deux espèces de conifères retenues varient en taux de croissance et en tolérance à l'ombre. Il était attendu que les espèces tolérantes à l'ombre auraient des meilleurs taux de survie dans la végétation herbacée que les espèces intolérantes à l'ombre, mais des taux de croissance inférieurs. Nous croyions aussi que la prédation serait plus importante sur les arbres poussant dans la végétation ou entourés de paillis, car les petits mammifères y seraient davantage à l'abri de leurs prédateurs que dans les parcelles sans végétation. Cette dernière hypothèse s'est confirmée sur le terrain. La prédation était la principale cause de mortalité. Les espèces les plus vulnérables furent les espèces de bouleau. La végétation herbacée a eu des effets négatifs (compétition) sur la survie des deux espèces non-pionnières et modérément tolérantes à l'ombre, des effets positifs (facilitation) sur la survie de l'espèce de conifère au système racinaire superficiel (mélèze laricin) et principalement des effets neutres (tolérance) sur la survie des cinq autres espèces d'arbres. Elle a eu des effets de compétition sur la croissance de toutes les espèces feuillues et pour la croissance des conifères, elle a eu des effets de facilitation ou encore aucun effet (tolérance).

Dans le dernier volet de la thèse, nous avons étudié les effets des microbes de sol forestier sur des arbres plantés en champ. Plusieurs microorganismes tels que les mycorhizes facilitent la croissance des plantes et des arbres. Comme certaines espèces, e.g. champignons

ectomycorhiziens, sont moins abondantes et diverses dans les sols des terres agricoles abandonnées, elles pourraient être inoculées en ajoutant du sol forestier et avoir un effet positif sur les jeunes arbres plantés. Parmi les communautés de sol forestier se trouvent toutefois des organismes pathogènes qui, selon l'hypothèse de Janzen-Connell, sont partagés entre des semis et des individus matures d'une même espèce. Afin de tester ces hypothèses, nous avons ajouté autour de jeunes arbres plantés en champ de petites quantités de sol issu de différentes forêts dominées par des arbres de la même espèce que les arbres plantés en champ ou encore dominées par une autre espèce. Nous en avons évalué les effets sur la survie et la croissance des arbres ainsi que sur la colonisation mycorhizienne des racines. Tel qu'attendu, la croissance des espèces d'arbres ectomycorhiziennes a davantage été influencée par l'ajout de sol forestier que celle des espèces endomycorhiziennes. Toutefois, peu d'effets ont persisté au-delà de la troisième saison de croissance. Ces résultats sont probablement dus au fait que l'ancien champ utilisé pour l'étude était d'une part, dominée par des espèces herbacées endomycorhiziennes et d'autre part, relativement fertile en possédant des taux élevés en phosphore. La croissance d'une seule espèce d'arbre (chêne rouge) a été négativement affectée par l'inoculation de sol collecté sous des individus de la même espèce, ce qui tend à confirmer que l'hypothèse de Janzen-Connell n'est pas aussi commune en forêt tempérée qu'en forêt tropicale.

En somme, cette thèse démontre que les interactions biotiques affectant les jeunes arbres influencent le succès de la restauration forestière et que les techniques de restauration utilisées doivent être adaptées selon les caractéristiques des espèces d'arbres et les conditions environnementales. Elle propose également que la restauration doit être planifiée à l'échelle du semis plutôt qu'uniformément à l'échelle du site, dans une optique de restauration de précision.

Mots Clefs : Terres agricoles abandonnées, restauration, plantation d'arbres, ensemencement, germination, établissement, survie, croissance, prédation, facilitation, tolérance, compétition, microorganismes de sol, mycorhizes, rétroaction négative, hypothèse de Janzen-Connell.

INTRODUCTION

0.1 Terres agricoles abandonnées

Depuis des millénaires, l'humain a coupé des arbres et défriché les terres afin de les cultiver. En Amérique du Nord, la colonisation et la culture des terres remontent toutefois à quelques centaines d'années seulement (Ramankutty et Foley, 1999a). Puis, une révolution verte s'instaurant dès la fin de la deuxième guerre mondiale, mais s'imposant dans les années 1970, transforme radicalement les méthodes de culture en proposant l'utilisation de nouvelles semences, de fertilisants, de pesticides, d'irrigation et de machinerie lourde (Rosset, 2000). Cette intensification et cette industrialisation de l'agriculture ont mené à l'abandon de terres agricoles plus marginales au courant des dernières décennies (Domon *et al.*, 1993; Ramankutty et Foley, 1999a, 1999b; MacDonald *et al.*, 2000). Par exemple dans le sud-ouest québécois, les techniques de drainage et l'utilisation de la machinerie lourde ont favorisé une transition des cultures vers les sols argileux mal drainés au détriment des terres agricoles sur sols caillouteux bien drainés (Domon et Bouchard, 2007).

Les terres agricoles abandonnées ont été particulièrement nombreuses dans le nord-est de l'Amérique comme par exemple dans le sud de l'Ontario et du Québec (Ramankutty et Foley, 1999b). L'abandon des cultures et pâturages est aussi observé en Europe et en Asie (Hunziker et Kienast, 1999; Ramankutty et Foley, 1999b), en Australie (Sun *et al.*, 1995; Doust et al. 2006; 2008), en Amérique centrale (Hooper *et al.*, 2002, 2005), en Amérique du Sud (Engel et Parrotta, 2001; Sampaio *et al.*, 2007) ainsi que dans les régions où l'on pratique l'agriculture sur brûlis (e.g. Bonilla-Moheno et Holl, 2010).

Certaines terres abandonnées sont recolonisées par la forêt (Ramankutty et Foley, 1999a, 1999b; Hunziker et Kienast, 1999). Dans d'autres cas toutefois, les communautés herbacées ou arbustives inhibent l'établissement et la croissance des arbres pendant de nombreuses années (Niering et Goodwin, 1974; Benjamin *et al.*, 2005). La succession végétale sur les terres agricoles abandonnées peut également être influencée par l'utilisation passée du site (de Blois *et al.*, 2001). Ainsi, la succession suite à l'abandon d'un pâturage diffère de celle suite à l'abandon d'un champ en culture (Stover et Marks, 1998; Benjamin *et al.*, 2005). Par exemple, les anciens pâturages sont plus propices à une végétation ligneuse, arbustive ou arborescente, comme les espèces de pommiers, poiriers, nerpruns et aubépines qui ont pu s'établir en raison d'un broutage sélectif (Stover et Marks, 1998).

La colonisation des terres agricoles abandonnées par les arbres demeure néanmoins limitée par la fragmentation des îlots forestiers résiduels et par une absence de géniteur (McEuen et Curran, 2004). Le nombre de graines et le nombre d'espèces présentes dans la pluie de semences et la banque de semences du sol diminuent en fonction de la distance à une forêt adjacente (Zimmerman *et al.*, 2000). Dans le nord-est américain, les espèces d'arbres qui colonisent les friches herbacées sont souvent des espèces pionnières dont les graines sont facilement dispersées par le vent comme le peuplier faux-tremble, le bouleau gris, l'érable rouge, le frêne d'Amérique et le frêne rouge (Hill *et al.*, 1995; D'Orangeville *et al.*, 2008). Les espèces barochores qui ont des graines plus volumineuses comme les chênes, les caryers et les noyers, se retrouvent rarement dans la strate de régénération des terres agricoles abandonnées et somme toute, la diversité arborescente y demeure assez faible (D'Orangeville *et al.*, 2008). Cependant, les espèces exotiques sont fréquentes. Dans les vieux champs abandonnés du nord-est américain, elles peuvent représenter jusqu'à un tiers des espèces herbacées et un quart des espèces ligneuses (Stover et Marks, 1998).

0.2 Restauration forestière

En raison de leur susceptibilité aux espèces exotiques envahissantes, de la lente succession végétale et de la faible diversité arborescente qu'on y retrouve, les terres agricoles abandonnées offrent un grand potentiel de restauration écologique. La restauration

écologique telle que définie par la « Society for Ecological Restoration International Science & Policy Working Group » (2004) est un processus qui initie, assiste ou accélère le rétablissement d'un écosystème qui a été dégradé, endommagé, transformé ou détruit directement ou indirectement par l'activité humaine. En un sens, c'est la manipulation des processus de succession dans le but de réaliser des objectifs de restauration de paysages perturbés (Hobbs *et al.*, 2007). En outre, les activités de restauration peuvent être utilisées dans le but d'améliorer ou de soutenir les biens et services, incluant les préférences sociétales et esthétiques (Hobbs et Norton, 1996). Une étude québécoise a montré que les terres abandonnées dominées par les herbacées ou les arbustes sont généralement mal perçues et peu appréciées par les habitants des paysages ruraux (Benjamin et al. 2007). Les auteurs suggèrent de convertir ces milieux en plantations forestières qui bénéficient d'une perception plus positive (Benjamin *et al.*, 2007). Par ailleurs, la majorité des personnes interrogées dans le cadre d'une étude sur les perceptions de l'afforestation des vieux champs des Alpes Suisse préfère des paysages partiellement reboisés et très diversifiés plutôt que de grandes parcelles forestières homogènes (Hunziker, 1995).

La restauration de terres agricoles abandonnées peut aussi contribuer à rétablir l'abondance de certaines espèces d'arbres. Par exemple, le hêtre à grandes feuilles, le bouleau jaune, la pruche du Canada, le mélèze laricin et l'épinette noire font partie de ces espèces qui étaient autrefois plus fréquentes dans le domaine climacique aujourd'hui dominé par l'érablière à caryer (Brisson et Bouchard, 2003; Domon et Bouchard, 2007).

0.3 Interactions biotiques

La compréhension des interactions biotiques entre les plantes herbacées, les herbivores, les microorganismes des sols et les arbres peut aider à bien planifier les plantations forestières menées dans un objectif de restauration des terres abandonnées. Les arbres sont sujets à plusieurs interactions positives, telles que la facilitation et le mutualisme, neutres (tolérance) et négatives, telles que la compétition, la prédation et la pathogénicité. Les relations peuvent varier en fonction des espèces en interaction, de leur cycle de vie, mais aussi en fonction des conditions abiotiques du milieu. Savoir par exemple dans quelles

conditions les interactions entre plantes et semis d'arbres sont positives ou négatives permet de faire une utilisation appropriée des techniques de maîtrise de la végétation herbacée.

0.3.1 Facilitation, tolérance et compétition

Les relations entre les arbres et les plantes herbacées évoluent de la facilitation à la compétition. La **facilitation** réfère aux interactions positives ayant lieu entre des plantes physiologiquement indépendantes, mais qui sont reliées à travers un environnement abiotique ou par d'autres organismes (Brooker *et al.*, 2008). Les bénéfices de la facilitation seraient plus importants dans des milieux où les conditions de croissance sont plus difficiles comme les déserts, les toundras, les milieux alpins, etc. (Brooker *et al.*, 2008; Gómez-Aparicio, 2009). De plus, la facilitation s'observerait davantage dans les milieux secs, mais si l'eau redevient disponible, la relation peut en devenir une de compétition (Holmgren *et al.*, 1997). En fait, selon l'hypothèse du gradient de stress (*stress-gradient hypothesis*), la facilitation a lieu principalement dans les environnements rigoureux alors que la compétition est présente dans les environnements plus productifs (Bertness et Callaway, 1994; Callaway et Walker, 1997).

Les effets de facilitation, comme une augmentation des taux de germination et de survie, une meilleure croissance ou une amélioration de la valeur adaptative (*fitness*) des semis (Callaway, 1997), peuvent être produits par la canopée de plantes protectrices ou en anglais « nurse plants » (Callaway et Walker, 1997; Holmgren *et al.*, 1997; Padilla et Pugnaire, 2006). Ces plantes, souvent des arbustes, permettent d'offrir un milieu plus ombragé et plus humide à d'autres plantes qui ne pourraient pas se développer sans elles. Le concept de « nurse plants » est aujourd'hui utilisé dans différents milieux avec d'autres types de facilitation pour les plantes et semis de leur voisinage. Par exemple, certaines favorisent la protection contre la prédation (e.g. des arbustes épineux qui protègent les semis du broutage), les échanges de nutriments (e.g. des légumineuses qui fixent l'azote) ou l'attrait des pollinisateurs (Benjamin *et al.*, 2005; Padilla et Pugnaire 2006). Les arbustes peuvent aussi protéger les semis d'arbres contre l'envahissement des communautés herbacées (Callaway et Walker, 1997; Padilla et

Pugnaire, 2006), bien que les plantes herbacées n'aient pas nécessairement un effet négatif sur les jeunes arbres.

Selon une méta-analyse faite par Gómez-Aparicio (2009), la végétation herbacée voisine a généralement un effet positif sur l'émergence des arbres, mais pour la survie et la croissance, les relations neutres ou négatives prédominent. La présence de la végétation herbacée facilite la germination de certaines espèces aux grandes semences comme le frêne et l'érable en offrant un microenvironnement plus humide qu'un sol à nu (De Steven, 1991a). Elle peut aussi augmenter les probabilités de survie des semis d'érable à sucre (Berkowitz *et al.*, 1995) et n'avoir aucun effet sur la survie du frêne rouge, du frêne d'Amérique et du chêne rouge (Labrecque, 2002; Robitaille, 2003). La facilitation de la survie ne suivrait donc pas l'hypothèse du gradient de stress (SGH) puisqu'elle peut avoir lieu dans des environnements productifs alors que la facilitation de la croissance est habituellement restreinte aux environnements plus difficiles (Goldgerg *et al.*, 1999).

Selon Grime (1977, 2007), la **compétition** serait aussi influencée par l'environnement car elle serait moins importante dans les milieux peu productifs car il y a moins de compétiteurs. Selon Tilman (1982, 2007), la compétition est présente dans tous les environnements, mais la ressource pour laquelle les plantes se font compétition change selon le niveau de productivité (e.g. la lumière dans les environnements productifs ou les ressources du sol dans les environnements moins productifs). La compétition se caractérise par son intensité, son importance et sa durée. L'intensité de la compétition réfère à l'effet absolu d'une plante sur une autre (Welden et Slauson, 1986). Selon Grime, l'intensité augmente donc plus il y a de ressources (milieux productifs) et selon Tilman, l'intensité pourrait être grande même dans les milieux pauvres. Les conclusions des travaux menés par Davis *et al.* (1998) penchent davantage du côté de Tilman que du côté de Grime en montrant que l'intensité de la compétition serait inversement corrélée à l'offre des ressources. Ils ont observé que l'intensité de la compétition par la végétation herbacée sur des semis de chêne était plus grande lorsque la biomasse herbacée et l'humidité du sol était faibles.

L'importance de la compétition réfère quant à elle à l'effet relatif d'une plante sur une autre en incluant tous les autres facteurs environnementaux pouvant affecter la plante (Welden et Slauson, 1986). Ainsi, l'étude de Laliberté (2006) a montré que malgré une grande biomasse herbacée, la compétition pour l'eau ne fût pas un facteur limitant la croissance de l'érable à sucre, du frêne rouge et du chêne à gros fruits plantés en champ en raison de l'absence de stress hydrique. La croissance de ces semis a plutôt été limitée dans les zones moins élevées du champ qui avaient une trop grande humidité (Laliberté, 2006).

La durée de la compétition serait plus importante que l'intensité initiale de compétition en étant relative au temps requis pour qu'un semis dépasse la canopée herbacée ou arbustive (Hill *et al.*, 1995). En milieu tropical, les espèces d'arbres ensemencées en champ qui ont de larges semences et qui sont modérément à hautement tolérantes à l'ombre germent et survivent bien sous le couvert herbacé (Hooper *et al.*, 2002; Doust *et al.*, 2006). Cependant, leur croissance relativement lente retarde la restauration du site alors que les espèces de début de succession, ayant généralement de petites semences, peuvent croître rapidement au-delà de la canopée herbacée, mais leur établissement est limité par la compétition herbacée (Doust *et al.*, 2008).

Au-delà de la compétition, se trouve l'**allélopathie** qui se définit comme l'effet néfaste d'une plante sur une autre via la production de composés chimiques libérés dans l'environnement (Horsley, 1977; Fisher *et al.*, 1978). Certaines espèces herbacées formant de denses communautés comme les verges d'or, les asters ou l'érigéron du Canada (*Erigeron canadensis*) auraient la capacité de produire des substances toxiques (Fisher *et al.*, 1978 ; Monk, 1983). Burton et Bazzaz (1995) ont observé que les communautés de verge d'or diminuaient la capacité photosynthétique des semis d'arbres et leur efficacité d'utilisation de l'eau, en réduisant la disponibilité de NO_3 dans le sol. En raison d'un manque de répétabilité des résultats des expériences et d'absence d'explications précises du rôle des composés chimiques émis, les effets allélopathiques des plantes herbacées des champs sur les semis d'arbres demeurent pour le moment hypothétiques (de Blois *et al.*, 2004).

Au milieu du gradient facilitation – compétition se trouve la **tolérance** qui réfère à l'absence d'effet apparent des plantes sur les semis d'arbres. Cependant, la tolérance peut aussi résulter de la somme nulle des effets négatifs et des effets positifs de la végétation herbacée sur les jeunes arbres. La facilitation, l'inhibition (reliée aux effets de compétition) et la tolérance se retrouvent dans les trois scénarios de succession proposés par Connell et Slatyer (1977). Dans le modèle de facilitation, les espèces de début de succession (e.g. les communautés herbacées) modifient l'environnement de façon à le rendre plus approprié pour les espèces de succession avancée (e.g. les arbres). Dans le modèle d'inhibition, les espèces pionnières (les plantes herbacées) accaparent l'espace et les ressources de sorte qu'elles inhibent l'établissement des espèces arborescentes ou ralentissent la croissance de celles qui sont déjà là. Finalement, dans le modèle de la tolérance, les modifications de l'environnement faites par les espèces pionnières n'augmentent pas et ne diminuent pas les taux d'établissement et de croissance des espèces de succession tardive, mais celles-ci poussant plus lentement et vivant plus longtemps, elles remplacent éventuellement les espèces pionnières (Connell et Slatyer, 1977). Partageant des mécanismes communs, comme la réduction de croissance ou la tolérance aux ressources limitées, les deux derniers modèles ne seraient pas entièrement distincts et des alternances entre les trois modèles existent au courant du cycle de vie d'une espèce (Pickett *et al.*, 1987 ; De Steven, 1991b). En effet, la facilitation, la tolérance et la compétition peuvent être présents au sein d'une même communauté végétale dépendant des conditions (Holmgren *et al.*, 1997). Des transitions entre la facilitation et la compétition de deux espèces peuvent se faire pendant leur cycle de vie, un changement de taille ou de densité d'une des espèces, ou un changement des conditions environnementales (lumière, humidité, etc.) engendrant un stress abiotique (Wootton, 1994; Callaway et Walker, 1997).

Les interactions entre plantes sont souvent complexes et indirectes (Wootton, 1994). Il n'est donc pas clair quand la végétation en place doit être enlevée, maîtrisée ou conservée (Gómez-Aparicio, 2009). En outre, les interactions indirectes entre deux espèces peuvent être dues à une troisième espèce et peuvent aussi inclure des interactions avec les ennemis ou les ennemis des ennemis (Wootton, 1994). Par exemple, qu'elle ait une relation de compétition

avec les arbres ou non, une végétation herbacée laissée intacte autour des jeunes arbres pourrait davantage affecter leur survie s'ils ne sont pas protégés de la prédation.

0.3.2 Prédation

Les petits mammifères comme les lapins et les campagnols peuvent induire de sérieux dommages aux semis en rongeant leur écorce ou en coupant leur tige (Stange et Shea, 1998; Pusenius *et al.*, 2000). La présence d'un couvert herbacé accroît habituellement les taux de **prédation** des semences et des semis ainsi que les dommages causés par les petits mammifères en réduisant les risques que les herbivores et granivores soient vu par leurs propres prédateurs (Gill et Marks, 1991; Ostfeld et Canham, 1993; Manson et Stiles, 1998; Pusenius *et al.*, 2000). Habituellement, les campagnols s'attaquent aux espèces ligneuses durant l'hiver lorsque la nourriture provenant des plantes herbacées devient plus rare (Witmer et VerCauteren, 2001). Un couvert végétatif haut et bien développé réduit la compaction de la neige ce qui facilite leurs déplacements, et il augmente l'effet d'isolation ce qui réduit leurs risques d'engelures et de mort par le froid (Hambäck *et al.*, 1998). Une présence importante de campagnols a un effet négatif sur la survie des semis, mais un effet positif indirect sur la survie des semences des arbres puisqu'elles sont davantage mangées par les souris qui sont moins nombreuses et moins actives en présence d'une grande population de campagnols (Ostfeld *et al.*, 1997; Manson *et al.*, 2001).

En plus de la prédation par les petits mammifères, les semences d'arbres peuvent être consommées ou déplacées par les oiseaux (García *et al.*, 2005) et les invertébrés comme les fourmis (Garcia-Orth et Martinez-Ramos, 2008) alors que les semis peuvent aussi être sujets à l'herbivorie par les invertébrés (McPherson, 1993; Sobek *et al.*, 2009) et les grands mammifères comme le cerf (Moore *et al.*, 1999; Hester *et al.*, 2000). Sur certains sites où la population de cerf de Virginie est importante, l'utilisation de moyens de protection contre cet hervivore (exclos, manchons protecteurs) augmente grandement la survie et la croissance des arbres plantés alors que sur d'autres, elle n'est pas nécessaire (Stange et Shea, 1998; Laliberté *et al.*, 2006; Cogliastro *et al.*, 2006). La prédation par les cerfs peut être plus grande lorsque

les arbres sont entourés par un paillis que lorsqu'ils sont directement dans la végétation herbacée en rendant les arbres plus facilement repérables (Stange et Shea, 1998).

0.3.3 Mutualisme

L'évolution a été façonnée par les relations de symbiose comme le **mutualisme** qui est bénéfique pour les deux organismes en interactions. La grande majorité des plantes vertes terrestres vivent en symbiose mycorhizienne, définie par l'association d'un organisme photosynthétique et d'un champignon filamenteux (Fortin *et al.*, 2008). Les mycorhizes facilitent l'utilisation de l'eau et l'acquisition des nutriments par les plantes, qui en retour, fournissent aux champignons les sucres résidus de la photosynthèse (Smith et Read, 2008). Il existe deux types de mycorhizes qui s'associent aux espèces arborescentes. Chez les mycorhizes arbusculaires (ou endomycorhizes) (AM), le mycélium pénètre à l'intérieur des cellules racinaires des arbres alors que chez les ectomycorhizes (EM), le mycélium enveloppe les cellules de l'hôte plutôt que d'y pénétrer (Fortin *et al.*, 2008). Les champignons AM sont reconnus pour faciliter l'acquisition du phosphore par les plantes alors que les champignons EM facilitent davantage l'acquisition de l'azote et dans les deux cas, cette facilitation est plus grande lorsque les nutriments respectifs sont limités (Reynolds *et al.*, 2005; Smith et Read, 2008).

La majorité des champignons mycorhiziens ne sont pas spécifiques et un individu peut simultanément coloniser un grand nombre de plantes de la même espèce ou de différentes espèces (van der Heijden et Horton, 2009). Les champignons EM seraient davantage associés à un hôte spécifique que les champignons AM (van der Heijden et Horton, 2009). Les associations semblent aussi plus bénéfiques entre espèces ayant le même type de symbiose (EM *vs* AM). Des semis de *Quercus rubra* ayant germé près de *Quercus montana*, deux espèces EM, ont connu une augmentation de leur croissance, de leur taux d'infection mycorhizienne et de leur absorption d'éléments nutritifs comparativement à ceux ayant germé près d'*Acer rubrum*, une espèce AM, qui a plutôt engendré une réponse négative (Dickie *et al.*, 2002).

Les mycorhizes sont en interaction avec d'autres organismes du sol qui peuvent influencer leur performance, leur dispersion, leur germination, etc. (Fitter, 1985; Fitter et Garbaye, 1994). Par exemple, des bactéries stimulent la colonisation et la sporulation alors que des invertébrés participent à la dispersion des spores (Fitter et Garbaye, 1994). Par contre, des nématodes peuvent inhiber la dispersion des hyphes alors que les chytrides et les amibes peuvent faire du parasitisme (Fitter et Garbaye, 1994). Néanmoins, selon une méta-analyse menée par Hoeksema *et al.* (2010), la réponse des plantes (e.g. biomasse) à l'inoculation mycorhizienne est plus importante lorsque plusieurs espèces de mycorhizes sont inoculées, lorsque des microbes autres que des mycorhizes sont aussi ajoutés ou encore, lorsqu'un échantillon de sol entier est inoculé plutôt que lorsqu'une seule espèce mycorhizienne est inoculée.

La biocénose du sol a rarement été manipulée afin d'augmenter le succès de la restauration, mais selon certains chercheurs cela semble être une avenue prometteuse (Heneghan *et al.*, 2008; Harris, 2009; Hoeksema *et al.*, 2010) alors que d'autres se demandent dans quelle mesure les communautés microbiennes du sol influence réellement le succès de la restauration (Bever *et al.*, 2010). Par exemple, ajouter de petites quantités de sol qui contient les mycorhizes désirées serait une façon simple d'inoculer des mycorhizes à un site qui en manque (Schwartz *et al.*, 2006). Les activités agricoles prolongées diminuent l'activité microbienne dont l'abondance et la diversité mycorhizienne (Dick, 1992; Jonhson, 1993; Helgason *et al.*, 1998; Florentine et Westbrooke, 2004; Alguacil *et al.*, 2008). En effet, les mycorhizes arbusculaires (AM) sont plus diversifiées dans les sols forestiers tout comme les ectomycorhizes (EM), mais ces dernières sont également plus abondantes dans les sols forestiers que dans les sols agricoles (Helgason *et al.*, 1998; Berman et Bledsoe, 1998; Dickie et Reich, 2005). Ainsi, l'ajout de sol forestier autour d'arbres plantés en champ permettrait d'inoculer des mycorhizes et potentiellement d'autres microorganismes bénéfiques comme des bactéries fixatrices d'azote, ce qui pourrait avoir un effet de facilitation sur la survie et la croissance des arbres.

0.3.4 Pathogénicité

Les sols forestiers peuvent cependant abriter des organismes **pathogènes**, ce qui entraînerait plutôt des effets négatifs sur les jeunes arbres. Packer et Clay (2000) ont observé que l'accumulation des pathogènes *Pythium* spp. dans le sol récolté près d'individus matures de cerisier tardif (*Prunus serotina*) avait un effet négatif sur la survie des semis de la même espèce. Plus précisément, ils ont trouvé que la probabilité de survie des semis de cerisier tardif était plus faible lorsqu'ils poussaient en pot avec du sol pris à moins de 5 mètres d'un arbre mature que lorsqu'ils étaient dans un sol pris à 25-30 mètres (Packer et Clay, 2000). Leurs résultats viennent ainsi appuyer l'hypothèse de Janzen-Connell qui stipule que les arbres matures et les semis d'une même espèce ont des ennemis communs qui engendrent une rétroaction négative (*negative feedback*) sur l'établissement, la survie et la croissance des semis situés à proximité de l'arbre mère (Janzen, 1970; Connell, 1971). Les ennemis communs peuvent être des organismes herbivores (e.g. insectes, mammifères) ou des pathogènes foliaires, mais la rétroaction négative serait fréquemment causée par les communautés microbiennes du sol (Bever *et al.*, 2010; Mangan *et al.*, 2010). En effet, les pathogènes dans le sol augmentent en présence de leur hôte (Burdon, 1987), ce qui crée des conditions peu favorables pour la régénération intraspécifique, mais qui favorise la diversité (Bever *et al.*, 1997; Mills et Bever, 1998; Mangan *et al.*, 2010). Dans le même ordre d'idées, la croissance des semis de quatre espèces d'arbres tropicales était réduite lorsqu'ils poussaient dans un milieu avec un inoculum de sol intraspécifique comparativement à lorsqu'ils étaient dans un milieu avec un inoculum hétérospécifique (Mangan *et al.*, 2010).

Comme les sols forestiers abritent des organismes bénéfiques et des organismes pathogènes, il demeure difficile de prédire dans quelles conditions les avantages que procurent les communautés microbiennes du sol aux arbres supplantent les effets de rétroaction négative.

0.3.5 Les traits fonctionnels

Les traits fonctionnels des arbres, *i.e.* leurs caractéristiques reliées à leur performance évolutive qui déterminent leur capacité à survivre, se reproduire et se disperser (Shipley

2007), peuvent influencer les interactions biotiques. Les réponses (survie et croissance) des espèces d'arbres aux différentes expériences de cette thèse seront évaluées selon la taille de leurs semences, leur taux de croissance, leur tolérance à l'ombre ou leur type d'association mycorhizienne. Par exemple, la prédation des semences réduirait davantage la germination des espèces ayant des semences de moyenne ou grande taille comme l'érable, le frêne et le pin que les espèces ayant des petites semences (De Steven, 1991a). Toutefois, une autre étude a montré que les granivores ont eu peu d'impact sur l'établissement du chêne rouge et du chêne à gros fruits qui ont de larges semences (Laliberté *et al.*, 2008a). Comme cité précédemment, les espèces qui ne sont pas intolérantes à l'ombre ont des bons taux de germination et de survie sous couvert herbacé (De Steven, 1991a; Hooper *et al.*, 2002; Doust *et al.*, 2006; Laliberté *et al.*, 2008a). Un autre exemple est que les semis d'espèces EM retireraient davantage d'effets bénéfiques à l'inoculation de champignons mycorhiziens que ceux d'espèces AM (van der Heijden et Horton, 2009).

Les traits fonctionnels des plantes herbacées comme le cycle de vie ou le mode de reproduction principal peuvent aussi influencer la relation entre plantes et les arbres. En milieu tempéré, la germination des espèces arborescentes serait légèrement plus importante sous couvert d'herbacées vivaces que sous couvert d'herbacées annuelles ou bisannuelles (Gill et Marks, 1991). Certaines communautés herbacées sont plus compétitives que d'autres. En général, les graminées ont un effet plus négatif sur les arbres que les autres plantes herbacées (*forbs*) (Gómez-Aparicio, 2009). Les espèces de légumineuses améliorent quant à elles les taux d'accumulation d'azote (Knops et Tilman, 2000). Il est important d'établir quels groupes d'herbacées ont un effet facilitateur ou neutre et quels groupes ont un effet compétitif, car dans ce cas, une maîtrise de la végétation peut être nécessaire.

0.4 Objectifs généraux de la thèse

Cette thèse a pour but d'évaluer différentes stratégies de restauration afin de faciliter le reboisement de friches herbacées. En effet, combiner deux ou trois techniques de restauration permettrait d'accélérer le rétablissement d'un site dégradé (Engel et Parrotta, 2001, Florentine et Westbrooke, 2004). La thèse se divise en deux grands volets. L'objectif général

du premier volet consiste à étudier les interactions entre la végétation herbacée et les arbres ensemencés ou plantés sur une terre agricole abandonnée. L'emphase des deux premiers chapitres est mise sur les relations de compétition, tolérance et facilitation, mais aussi de prédation selon différents traitements de végétation. Le second volet de cette thèse s'attarde à évaluer les effets des microorganismes de sol forestier sur la survie et la croissance des arbres plantés en champ. L'effet global de l'inoculation de ces microorganismes sur les jeunes arbres est le résultat d'une équation qui inclut les effets négatifs dus aux espèces pathogènes et les effets positifs dus aux espèces mutualistes tels que les champignons mycorhiziens.

0.5 Objectifs spécifiques

Plusieurs chercheurs ont suggéré qu'ensemencer des arbres pour restaurer des terres dégradées constitue une stratégie moins coûteuse en temps et en argent que la plantation (Engel et Parrotta, 2001; Hooper *et al.*, 2002; Florentine et Westbrooke, 2004; Sampaio *et al.*, 2007). Cependant, les résultats de l'effet d'un couvert herbacé sur les taux de germination et de prédation des semences sont souvent contradictoires entre les études. En ce sens, nos premiers objectifs sont d'établir quelles espèces d'arbres ont une relation de compétition, tolérance ou facilitation avec la végétation herbacée et quelles espèces sont affectées par la prédation des semences ou des semis.

Les mêmes objectifs sont repris dans une expérience similaire où les arbres sont plantés plutôt qu'ensemencés. Encore une fois, nous désirons mesurer l'effet de la présence ou de l'absence de la végétation herbacée sur la prédation des plants et identifier quelles espèces sont le plus affectées par les petits mammifères. Nous voulons aussi évaluer comment la croissance des jeunes arbres est affectée par la végétation herbacée selon différentes conditions telles que le pourcentage de recouvrement et la hauteur des espèces herbacées ou encore l'humidité du sol, mais aussi selon les traits fonctionnels des espèces d'arbre.

En identifiant les conditions qui influencent le gradient compétition – facilitation entre les communautés herbacées et les espèces d'arbres ensemencés ou plantés en champ, ces études contribuent à la compréhension des processus de colonisation des espèces

arborescentes dans les milieux ouverts. D'un point de vue appliqué, elles permettent d'établir quelles espèces d'arbres bénéficient d'une protection contre les rongeurs et/ou d'une maîtrise de la végétation herbacée.

Le dernier objectif spécifique vise quant à lui à clarifier les conditions influençant le gradient pathogénécité – mutualisme entre les microorganismes du sol et les arbres. À notre connaissance, l'inoculation de microorganismes de sol forestier a rarement été faite sur des arbres plantés en champ. Cela a surtout été testé en pot ou encore sur des arbres destinés au reboisement en forêt qui étaient inoculés avec seulement une ou quelques espèces de champignons mycorhiziens. Nous voulons évaluer les effets des espèces microbiennes inoculées par l'ajout de sol forestier sur la survie et la croissance de jeunes arbres plantés en champ selon que les arbres soient d'espèce ectomycorhizienne ou endomycorhizienne. Nous voulons aussi savoir s'il y a plus d'effets positifs que d'effets négatifs et si les effets varient selon la provenance du sol ajouté (inoculum intraspécifique ou interspécifique) ainsi que la quantité de sol ajouté. Le sol forestier pourrait donc avoir un potentiel de facilitation pour la croissance des arbres en champ qui serait facile à utiliser et peu coûteux. Par ailleurs, cette étude nous permet de tester l'hypothèse de Janzen-Connell en champ plutôt qu'en pot, ce qui a peu été fait en milieu tempéré.

L'objectif appliqué de la thèse est d'améliorer le succès de la restauration forestière des terres agricoles abandonnées, mais les résultats pourront aussi être utilisés pour d'autres types de plantation en milieu ouvert comme pour la création de corridors forestiers.

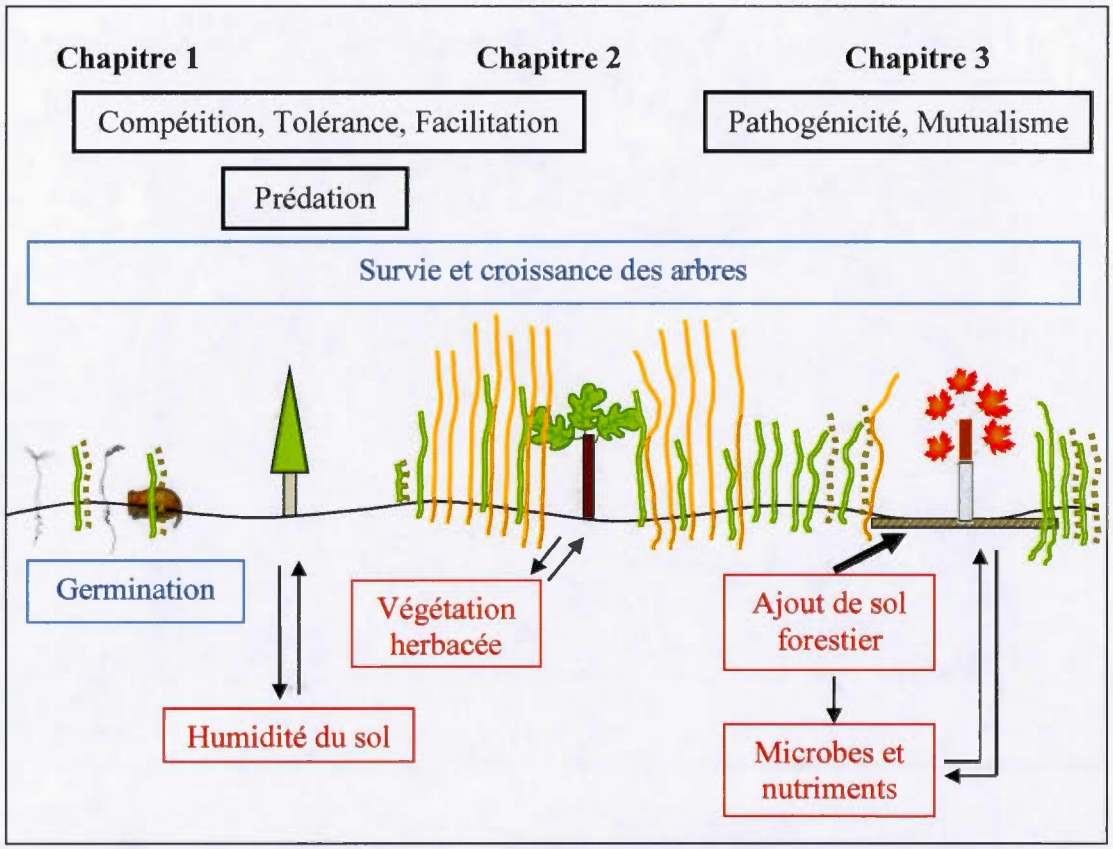

Figure 0-1 Schéma conceptuel de la thèse.

Figure 0-2 Localisation de l'aire d'étude, chapitres 1 et 2, Auteuil, Laval.

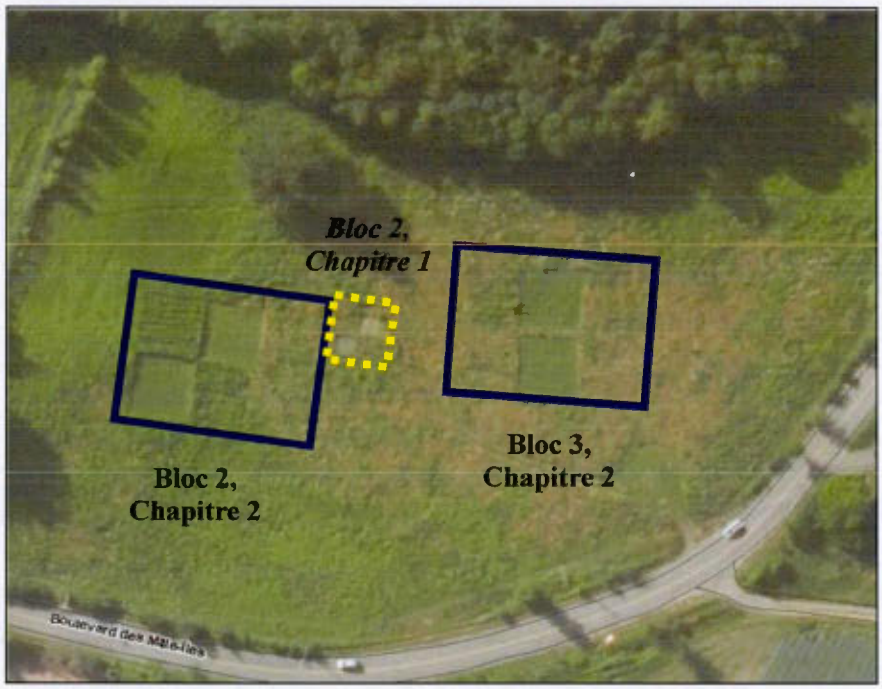

Figure 0-3 Localisation du bloc 2 (tirets) de l'expérience du chapitre 1, et des blocs 2 et 3 (lignes pleines) de l'expérience du chapitre 2, 2e année (2011).

Figure 0-4 Localisation de l'aire d'étude, chapitre 3, L'Assomption et des 5 blocs.

CHAPITRE I

1. SEED SIZE, THE ONLY FACTOR POSITIVELY AFFECTING DIRECT SEEDING SUCCESS IN AN ABANDONNED FIELD IN QUEBEC, CANADA

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Annick St-Denis, auteure principale
Centre d'étude de la Forêt, Département des Sciences Biologiques, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, Canada, H3C 3P8.
st-denis.annick.2@courrier.uqam.ca

Christian Messier
Centre d'étude de la Forêt, Département des Sciences Biologiques, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, Canada, H3C 3P8 ; Institut des Sciences de la Forêt Tempérée, Université du Québec en Outaouais, 58 rue Principale, Ripon, Canada, J0V 1V0.
messier.christian@uqam.ca

Daniel Kneeshaw
Centre d'étude de la Forêt, Département des Sciences Biologiques, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, Canada, H3C 3P8.
kneeshaw.daniel@uqam.ca

1.1 Abstract

Direct tree seeding is potentially an economical technique for restoring forests on abandoned fields. However, the success of tree establishment depends on many factors related to species and seed characteristics, environmental conditions, competition and predation. We compared seedling emergence, survival and growth of six tree species of different seed sizes in a forest restoration project of abandoned fields. Species were seeded in plots with and without herbaceous vegetation and with and without protection from bird and mammal predation. Yellow birch (*Betula alleghaniensis*) did not emerge in all treatments, paper birch (*Betula papyrifera*) and tamarack (*Larix laricina*) had a seedling emergence rate lower than 1%, and sugar maple (*Acer saccharum*) had a low overall emergence rate of 6%. Seedling emergence reached 57% for northern red oak (*Quercus rubra*) and 34% for red pine (*Pinus resinosa*), but survival of oak after one year was much higher (92%) than pine seedlings (16%). Overall, protection from birds and mammals and elimination of the herbaceous vegetation cover had no detectable effects on seedling emergence, survival and height. Nonetheless, red oak seedlings growing in the presence of vegetation had a smaller diameter and shoot biomass and a larger specific leaf area. We conclude that only large seeded species, such as oak, should be used for forest restoration of abandoned fields by direct seeding in our region.

Keywords: tree; direct seeding; seedling emergence; survival; growth; seed size; competition; predation

1.2 Introduction

Over recent decades, industrialisation and intensification of agriculture in occidental countries have led to agricultural fields in marginal environments being abandoned (MacDonald *et al.*, 2000; Ramankutty and Foley, 1991a, 1991b; Domon *et al.*, 1993). In these fields, herbaceous or shrub communities may inhibit tree establishment for many years (Niering and Goodwin, 1974; Benjamin *et al.*, 2005), and tree recruitment is dominated by a few wind-dispersed pioneer species (D'Orangeville *et al.*, 2008; Hill *et al.*, 1995). In both temperate and tropical ecosystems, direct seeding has been proposed as a time- and cost-effective technique to restore abandoned fields; indeed, tree plantations may cost 1.5 to 2.5-times the cost of direct seeding (Bullard *et al.*, 1992; King and Keeland, 1999; Engel and Parrotta, 2001; Hooper *et al.*, 2002; Sampaio *et al.*, 2007). However, many endogenous factors, such as the type and density of competing vegetation, the presence or not of predation, soil type and exogenous factors, such as climatic conditions, interact with seed size and shade tolerance to affect the overall success of this technique (De Steven, 1991a; Gill and Marks, 1991; Burton and Bazzaz, 1991; Hooper *et al.*, 2002; Doust *et al.*, 2006). Although many studies have been conducted to investigate the success of direct seeding as a way to restore abandoned fields, few have attempted to evaluate the interacting effects of herbaceous vegetation (both positive and negative) and predation across a wide range of tree species in temperate ecosystems (but, see De Steven, 1991a; Gill and Marks, 1991; Burton and Bazzaz, 1991).

Effects of vegetation (both positive and negative) on seedling emergence vary with plant litter (Myster, 1994) and surrounding vegetation types (Burton and Bazzaz, 1991). In general, grasses have more negative effects and are stronger competitors than forbs (Gómez-Aparicio, 2009). For examples, *Poa pratensis* communities constitute a less conducive environment to tree seedling emergence, except for *Crataegus mollis*, while many other types of vegetation were not found to have an impact on the emergence of *Acer saccharum* (Burton and Bazzaz, 1991). Although herbaceous vegetation can have a positive, neutral or negative effect on seedling emergence, it usually has a negative impact on seedling growth (Gómez-Aparicio, 2009). In the studies conducted by De Steven (1991a, 1991b), even if herbaceous cover had a

positive effect on the emergence of species with larger seeds (*Fraxinus americana* and *Acer rubrum*), it had negative impacts on seedling survival and growth of all five species tested (De Steven, 1991b).

Seedling predation can be more important than competition as a factor affecting overall tree survival in seeding experiments. In the Northeastern US, Gill and Marks (1991) showed that seedling mortality was essentially due to predation by voles rather than herbaceous competition and that predation was more important under herb cover. Vegetative cover, in fact, increases the probability of seedling damage caused by small rodents, because it decreases the risk of small mammals being seen by their own predators (Ostfeld and Canham, 1993). Meadow voles (*Microtus pennsylvanicus*) are important seedling predators, whereas white-footed mice (*Peromyscus leucopus*) are large seed consumers (Ostfeld *et al.*, 1997; Manson *et al.*, 2001). Fortunately, their negative impacts are rarely simultaneous, because mice are less abundant in fields when vole populations are high, and they are more active when vole density is low (Ostfeld *et al.*, 1997; Manson *et al.*, 2001). *Muridae* and *Cricetidae* are not the only types of seed and seedling predators; squirrels, rabbits, deer, cattle, wild boars, birds and insects, such as ants, may also affect the success of seedling establishment via predation (Herrera, 1995; Kollmann and Schill, 1996; Hulme and Borelli, 1999; Woods and Elliott, 2004). The wide range of predator sizes probably explains in part why Moles *et al.* (2003) found no significant relationship between seed mass and seed predation in their literature review.

The objectives of this study were: (1) To measure seedling emergence, survival and growth of six tree species of different seed size and shade tolerance directly sown in an abandoned field; and (2) To evaluate the effects of herbaceous vegetation, predation and their interactions on seedling emergence, survival and growth. We hypothesize that seedling emergence and survival rates will increase with increasing seed size. We suppose that vegetation will enhance seedling emergence of the shade tolerant species evaluated in our study (sugar maple), have no impact on the emergence of the large-seeded mid-shade tolerant species (red oak) and have a negative effect on the emergence of small-seeded shade

intolerant species. We also hypothesize that vegetation cover will have neutral or negative effects on seedling survival and growth and that predation will be higher under a vegetation cover.

1.3 Methods

1.3.1 Study area

The study took place in three abandoned fields located in southwestern Québec (Canada), in the agricultural zone of Laval (45°40′N; 73°43′W), north of Montréal. The region is characterized by a humid continental climate. During the study, the average annual temperature recorded at the Montréal weather station was 8 °C, with monthly means of 23 °C in July and −10 °C in January (Environment and Climate Change Canada, 2013a, 2013b). The annual precipitation varied between 1194 mm (2010) and 1281 mm (2011) (Environment and Climate Change Canada, 2013a, 2013b). A 3.5 ha forest, dominated by *Acer saccharinum* and composed of *Fraxinus nigra*, *Fraxinus pennsylvanica*, *Populus deltoides* and *Thuja occidentalis* separates the first two fields from the third. The surficial deposits are mainly of glacial origin. A stony clay loam soil is found on the first two fields, while the soil in the third field is a clay loam (IRDA, 2008).

Fields one and three have an area of about 9000 m^2, while the second field is bigger, with an area of about 23,000 m^2. The three abandoned fields had a similar past land use and were cultivated for at least 25 years. In the early 2000s, cultivation stopped, but the sites were mown once or twice a year, until the fall of 2009. This mowing prevented tree and shrub establishment and promoted ruderal herbaceous vegetation. Fields had sufficiently similar conditions to establish a split-plot design of three randomized blocks (see next section), with one block per field. However, herbaceous vegetation differed somewhat between blocks. In the first one, the vegetation was principally dominated by grass species (*Poaceae* spp. and *Cyperaceae* spp.), *Solidago* spp., *Trifolium repens* and *Trifolium pratense*. The vegetation in the second plot was also dominated by grasses, but associated species were *Taraxacum officinale*, *Sonchus oleraceus* and *Medicago lupulina*. In the third plot, *Solidago* spp. were as

important as grass species, and *Taraxacum officinale*, *Sonchus oleraceus*, *Medicago lupulina* were also abundant. Total ground coverage by all species was around 70% in each plot.

1.3.2 Experimental design

The study took place between May, 2010, and August, 2011. In each field, a 9 × 9 m experimental block was installed at least 20 m from the forest, trees bordering the fields and a road, to avoid edge effects. Experimental blocks were divided into four plots following a split-plot design, where the main factor was "protection" (protection of seeds and seedlings from predation or no protection), and the subplot factor was "vegetation" (intact herbaceous vegetation or bare soil). Protection from rodents was achieved using a surrounding exclosure fence of 6 mm mesh and 120 cm high. The bottom part of the fence was curved, nailed into the ground and covered with stones and soil instead of buried, due to soil compaction. Fishing lines were placed on the top of the protected area, every 10 cm, to prevent birds from entering into these plots. Fishing lines had no effect on light transmission; percentages of photosynthetic photon flux density (%PPFD) were similar in plots with or without protection. Deer could have jumped into the protected area, breaking fishing lines, but no sign of deer damage was seen.

Vegetation on half of the protected and unprotected plots was maintained. On the other half, all vegetation was weeded by hand before the beginning of the experiment. From June, 2010, to August, 2011, vegetation was regularly cut by scissors in the sown locations instead of weeded by hand, to avoid soil disturbance around seeds and small seedlings. In rows between sown locations, vegetation was weeded by hand until the end of August, 2010. By this time, almost all seedling emergences occurred; thus, coconut fiber mulches were put between sown locations to reduce weeding time.

1.3.3 Seeding

Each subplot contained ten sown locations per species, spaced 30 cm apart. The six species used in this study were chosen, because they are native to the area, and they differed in seed size and shade tolerance (Table 1.1). They were: paper birch (*Betula papyrifera*),

yellow birch (*Betula alleghaniensis*), tamarack (*Larix laricina*), red pine (*Pinus resinosa*), sugar maple (*Acer saccharum*) and northern red oak (*Quercus rubra*). Seeds were prepared and provided by the Centre des semences forestières de Berthier (CSFB) from the Quebec Ministry of Natural Resources. Usually, all of these species are sown in the spring, except acorns of northern red oak, which are sown in the autumn. Acorns were thus placed in a cold room (4 °C) from November, 2009, to May, 2010, so they could also be sown in the spring. Yellow birch seeds needed stratification for 21 days, while sugar maple seeds spent two weeks in cold water, followed by stratification for 3.5 weeks. Other species did not require special treatment preceding spring seeding. Seed germination in the laboratory, determined by professionals from the Quebec Ministry of Natural Resources, was more than 80% for all species (Table 1.1). Seeds were kept in a dark cold room (4 °C) until seeding from 25 to 27 May, 2010. The number of seeds in each sown location decreased with seed size, as the production of seeds in nature is usually higher for small-seeded species than for large-seeded species. Five seeds of paper birch and five of yellow birch were used (total of 600 seeds/species), four seeds of sugar maple, red pine and tamarack (total of 480 seeds/species) and three acorns of red oak (total of 360 acorns). Seeds were buried at a depth of 0.5 to 5 cm, depending on seed size and following recommendations given by professionals from the Quebec Ministry of Natural Resources.

1.3.4 Measurements

1.3.4.1 Seedling emergence, survival, and growth

Seedling emergence, survival and height were measured every week between 21 June and 14 July, 2010, at the end of July and August, 2010. Sampling was also conducted once in May, 2011, and twice in June, 2011, to measure seedling height and seedling survival after the winter and to see if new seedlings emerged one year after seeding. Seedling emergence refers to the proportion of seedlings emerging in a sown location. We use the term proportion of live seedlings as the number of seedlings emerged per number of seeds buried. Seedling survival for 2010 was calculated as the proportion of live seedlings at the end of August, 2010, out of the proportion of live seedlings at the end of June, 2010. Seedling survival after one year is calculated as the proportion of live seedlings in June, 2011, out of the maximal

proportion of live seedlings in 2010. Height was measured as the distance between the soil surface and the apical meristem, but for red pine, we measured height until the end of the needles.

1.3.4.2 Red oak seedling measurements

Additional measures were taken on red oak seedlings in August, 2011, to measure the effects of competing vegetation on different variables related to growth. At this time, pine and maple seedlings were not sufficiently abundant to make comparisons between treatments. To avoid intraspecific competition between oak seedlings, we kept only one seedling per sown location at the beginning of July 2011. We randomly chose among averaged size seedlings in good shape. Height, diameter, shoot biomass and specific leaf area (SLA) were measured on five red oak seedlings randomly chosen in each subplot (n = 60 seedlings). No belowground measures were taken, due to the high compaction of the soil. Specific leaf area (SLA) was measured following the method described by Cornelissen *et al.* (2003). Two healthy leaves per seedling were taken and were scanned the day of collection. Leaf area was calculated using the Winfolia software (Régent Instruments, Québec, QC, Canada). Leaves were dried at 70 °C for at least 48 h before their mass was measured. We also calculated relative height growth rate (RGR_H) using the formula:

$$RGR_H = \frac{\ln(H2) - \ln(H1)}{t}$$

where $H2$ corresponds to height in August 2011, $H1$, height in August 2010, and t, time between both measures, which is one year.

Table 1-1 Characteristics and seed germination in the laboratory of the six tree species tested

Species	Species development in natural conditions	Average dry seed mass (g)	Shade tolerance	Germination in laboratory
Betula papyrifera Marsh. (Paper birch)	Fast-growing tree, often established after fire or logging; develops best on well-drained sandy loams	0.00045	Low	82%
Betula alleghaniensis Britton (Yellow birch)	Slow-growing tree, often found on moist well-drained soils	0.0012	Intermediate	88%
Larix laricina (Du Roi) K. Koch (Tamarack)	Fast-growing tree, often found on wet to moist organic soils	0.0027	Low	81%
Pinus resinosa Ait. (Red pine)	Moderate to fast growing tree, usually established following fire; often found on sandy soils	0.01	Low	93%
Acer saccharum Marsh. (Sugar maple)	Slow-growing tree; grows on a variety of sites and soils	0.06	High	88%
Quercus rubra L. (Northern red oak)	Moderate to fast growing tree; found on a variety of soils	3.14	Intermediate	88%

Species development in natural conditions (Burns and Honkala, 1990); average dry seed mass (CSFB, 2010; for red oak: Royal Botanic Gardens Kew, 2008); shade tolerance (Burns and Honkala, 1990; USDA, NRCS, 2013); rates of germination in the laboratory (CSFB, 2010).

1.3.4.3 Environmental measurements: soil moisture and light

During the summer of 2011, two sown locations per species were randomly chosen to take environmental measurements. Soil volumetric water content was measured at three

occasions using a TDR-200 probe (Spectrum Technologies Inc., Plainfield, IL, USA) with 12 cm rods. A mean value was obtained from two measurements taken in the middle of each sown location. The first series of measurements was taken on 15 June, two days after a rain of 10 mm and three days after a rain of 30 mm. The second measurements were taken on 12 July, after a light rain of 2 mm, and the third measurements were taken on 18 July, after a light rain of 1 mm. Photosynthetic photon flux density (%PPFD) was measured using point quantum sensors (LI-COR, Inc., Lincoln, NE, USA). Measurements were taken at the end of July, 2011, on cloudy days, following the method described in Messier and Puttonen (1995).

1.3.5 Data analysis

Linear regressions were used to test the relationship between seedling emergence and seedling survival as a function of seed size. Repeated measure ANOVAs, following a two-way split-plot design (described above), were computed to evaluate the effect of protection treatment, vegetation treatment, time and their interactions on the proportions of live seedlings and on soil volumetric water content. Analyses of variance of the proportions of live seedlings between treatments were also performed by date, following the same two-way split-plot design. Variances of seedling survival and height on 25 August, 2010 and 15 June, 2011 were analysed using the same statistical model. Blocks (n = 3) were considered as a random effect, and analyses were performed separately by species, due to the large differences between the proportions of live seedlings and seedling heights. Yellow birch, paper birch and tamarack were not included in the data analysis, because their seedling emergence was nonexistent or negligible. ANOVA was also used to compare light levels (%PPFD), which were log transformed to achieve normality. Finally, ANOVA was used to compare five growth variables of red oak seedlings between treatments following the same two-way split-plot design. For all analyses, we computed Tukey *post hoc* tests when a variable was found to be significantly affected by a treatment ($p \leq 0.05$). Statistical analyses were conducted using JMP software (version 10.0) (SAS Institute Inc., 2007).

1.3.6 Second seeding experiment

In 2011, we conducted a second seeding experiment to compare rates of seedling emergence between 2010 and 2011 for our best performing species (red oak, red pine and sugar maple) and to test another large-seeded species, bur oak (*Quercus macrocarpa* Michx.; dry seed mass of 6.15 g (Royal Botanic Gardens Kew, 2008); mid-shade tolerant species (USDA, NRCS, 2013). Once again, seed germination in the laboratory was higher than 80% for all species (CSFB, 2010). Unfortunately, we could not use the same site, because the fields were full of small trees planted in the summer of 2010. We thus used another site, located in the same area. The site was an abandoned old field recently disturbed by a residential development. Competing vegetation was sparse and dominated by *Equisetum* species, grass species and some *Cornus stolonifera* shrubs. The soil was composed of clay loam (IRDA, 2008).

Four experimental blocks were established in the field. Each block contained eight sown locations per species (for a total of 32), and 4 seeds by sown location were buried (for a total of 128 seeds/species). No vegetation or predation control was conducted. Seeding was done on 19 May and 25 May, 2011. The proportions of live seedlings were monitored four times in the summer of 2011 and once in the spring of 2012.

1.4 Results

1.4.1 Establishment success

Seedling emergence and, to a lesser extent, seedling survival increased with seed size ($R^2 = 0.63$, $p < 0.0001$; $R^2 = 0.47$, $p = 0.0006$, respectively). Despite having sown 600 seeds, no yellow birch seedlings emerged. Only one paper birch seedling emerged, in a plot with vegetation and protection, and it measured 15.5 cm in the summer of 2011. Five tamarack seedlings emerged at the beginning of July, but they died a few days after emergence. Seedling emergence of red pine reached a maximum of 34% at the end of June 2010 (Table 1.2). Over the summer, the needles of several pine seedlings changed color, from green to red-brown and decreased in length, until those pine seedlings died. Between the end of July

and the end of August, 2010, 22% of the pine seedlings decreased in height (measured until the end of live needles) and the average height declined from 4.2 to 4.0 cm. The same tendency was observed between August, 2010, and June, 2011: the average live height decreased from 4.0 to 3.8 cm, and 45% of the pine seedlings were smaller in 2011 than in August, 2010. At the end of the first growing season, only 52 pine seedlings out of 163 (survival of 32%) were still alive, while in the spring, 2011, the proportion of live seedlings was only 5.5%.

Seedling emergence of sugar maple reached a maximum of 5.8% at the beginning of July 2010 (Table 1.2). After one year, 57% of maple seedlings were still alive and their average height was 10.9 cm. Red oak emerged later than the other species, but had excellent survival. The maximum seedling emergence of 57.2% occurred at the end of August 2010 and as no oak seedlings died during the first growing season, we estimated its survival to be 100% in 2010. In the spring, 2011, the proportion of live seedlings was 52.5%, for a seedling survival of 92%, and their average height was 10.6 cm. Only one new red oak seedling and one new sugar maple seedling emerged in the spring, 2011.

In the second experiment, seedling emergences were 65.6% for red oak, 14.1% for sugar maple and only 3.9% for red pine, while seedling survival for each species after one year were 98.8%, 83.3% and 20.0%, respectively. Seedling emergence of bur oak was 60.9% in 2011. Only three bur oak seedlings died between 2011 and 2012, but 28 new seedlings emerged in the spring of 2012, for a maximum of 82.8% seedling emergence.

1.4.2 Effects of treatments

Repeated measures ANOVA showed no effect of treatments "protection" and "vegetation" on the proportions of live seedlings with time (Fig.1.1). Analyses of variance calculated by date showed only one significant effect. In the middle of July 2010, the proportion of live pine seedlings was higher in plots without vegetation (27.0%) than in plots with vegetation (7.8%) ($F_{1,2.22} = 44.33$, $p = 0.0165$; Fig. 1.1a). Mortality of pine seedlings started earlier in plots with vegetation, but this difference disappeared after two weeks. No

differences in variances were observed during the other weeks. Vegetation and protection treatments had no effect on seedling survival and seedling height of the three species. Moreover, no sign of predation on seeds or seedlings were seen in any plots, except for one sugar maple seed in a plot without vegetation and without protection.

At the end of the second summer, only red oak seedlings were numerous enough to make growth comparisons between treatments. *Post hoc* tests in the analysis of variance of five growth variables showed that vegetation significantly reduced red oak diameter and shoot biomass and increased specific leaf area (Table 1.3), while the protection treatment had no effect. Seedling height and relative height growth rate did not differ between treatments. Vegetation also had a negative effect on soil moisture ($p \leq 0.05$). Soil volumetric water content was higher in plots without vegetation, and this difference increased with time (Table 1.4). Repeated measure ANOVA showed an interaction between vegetation and dates (time) for soil moisture ($p < 0.0001$). Percentage of photosynthetic photon flux density (%PPFD) was lower under vegetation (23.1%) than on bare soil (88.3%) ($F_{1,1.97} = 3066.28$, $p \leq 0.05$).

Table 1-2 Seedling emergence, survival and height of red pine, sugar maple and northern red oak

Species	Date of maximum emergence	Maximum emergence (%)	Seedling survival in 2010 (%)	Seedling survival in 2011 (%)	Proportion of live seedlings in June 2011	Height in June 2011 (cm)
Red pine	21 June, 2010	34.0 ± 17.6	32.1	16.3	5.5 ± 5.9	3.8 ± 0.6
Sugar maple	6 July, 2010	5.8 ± 4.6	71.4	57.1	3.3 ± 3.1	11.5 ± 0.7
Red oak	25 August, 2010	57.2 ± 13.8	100	91.7	52.5 ± 14.8	10.6 ± 0.2

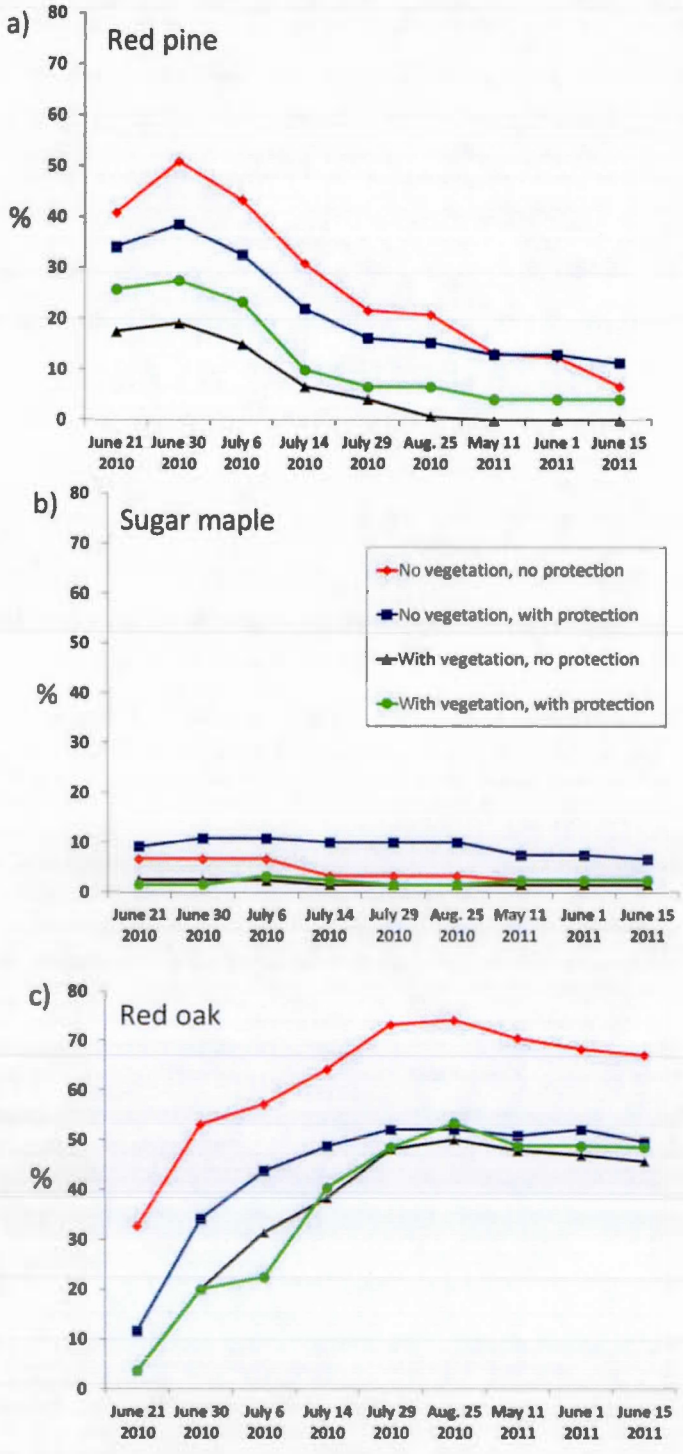
a)
Red pine
%
80
70
60
50
40
30
20
10
0
June 21 2010
June 30 2010
July 6 2010
July 14 2010
July 29 2010
Aug. 25 2010
May 11 2011
June 1 2011
June 15 2011
b)
Sugar maple
No vegetation, no protection
No vegetation, with protection
With vegetation, no protection
With vegetation, with protection
c)
Red oak

Figure 1-1 Mean percentage of live seedlings in response to treatments "vegetation" and "protection", between 21 June, 2010 and 15 June, 2011 for (a) red pine; (b) sugar maple; and (c) red oak. Sub-figures (a to c) ordered by species seed size.

Table 1-3 Effects of the presence of vegetation on five variables related to the growth of red oak seedlings in August, 2011

Growth variables	No vegetation	Vegetation	F_{df}; p-values
Height (cm)	10.65 ± 0.58	12.53 ± 0.57	$F_{1,1.98} = 7.82$; $p = 0.1086$
RGR_H (cm cm^{-1} yr^{-1})	0.50 ± 0.03	0.45 ± 0.03	$F_{1,1} = 0.0005$; $p = 0.9860$
Diameter (mm)	***3.51 ± 0.19***	***2.64 ± 0.19***	$F_{1,1.11} = 118.47$; $p = 0.0486$
Shoot biomass (g)	***1.36 ± 0.08***	***0.78 ± 0.07***	$F_{1,1.85} = 29.42$; $p = 0.0381$
SLA ($mm^2 \cdot mg^{-1}$)	***14.75 ± 0.53***	***17.13 ± 0.53***	$F_{1,1.96} = 21.24$; $p = 0.0456$

Values are the means ± standard errors (SE). Means and SE in bold and italics are significantly different at $p \leq 0.05$ according to ANOVA and *post hoc* tests. Measurements were taken at the end of August, 2011. RGR_H = relative height growth rate for one year; SLA = specific leaf area.

Table 1-4 Soil volumetric water content (%) within the first 12 cm of soil in the summer of 2011

Date	Precipitation during the last 3 days (mm)	No vegetation	Vegetation	F_{df}; p-values
15 June, 2011	41	***22.5 ± 0.4***	***21.1 ± 0.4***	$F_{1,2.08} = 21.42$; $p = 0.0405$
12 July, 2011	2	***22.4 ± 0.4***	***18.6 ± 0.4***	$F_{1,1.96} = 31.14$; $p = 0.0321$
18 July, 2011	1	***23.8 ± 0.5***	***17.3 ± 0.5***	$F_{1,2} = 83.39$; $p = 0.0117$

Values are the means (%) ± standard errors (SE). Means and SE in bold and italics are significantly different at $p \leq 0.05$ according to ANOVA and *post hoc* tests. There was a positive interaction between dates (time) and vegetation treatment ($p < 0.0001$).

1.5 Discussion

1.5.1 Establishment Success and Seed Size

Our field study confirmed the importance of seed size for seedling emergence and seedling survival in abandoned fields, despite high germination rates (>80%) of all species in laboratory trials. Other studies have also shown major differences between germination in controlled conditions (for example, a greenhouse) and seedling emergence in an abandoned field (De Steven, 1991a; Ray and Brown, 1995; Doust *et al.*, 2006, 2008), which is a harsh environment with wide fluctuations in temperature and moisture and often with compacted soils (Burton and Bazzaz, 1991; De Steven, 1991a). In our experiment, the lightest seeded species did not emerge even in the bare soil plots. Under natural conditions, the germination capacity of yellow birch is only about 20% (Burns and Honkala, 1990). Tests conducted, in an agricultural field at the government nursery have shown that seedling emergence attained only 20% for paper birch and 39% for yellow birch (CSFB, pers. comm.). Seedling emergence for these two species was lower than for species with higher seed mass, even if these soils were watered regularly and free of competition. This further confirms that larger seeded tree species emerge and survive better in the field than smaller seeded species.

A lack of soil moisture may be one of the main factors causing the failure of seedling emergence. However, according to Burton and Bazzaz (1991), temperature may be more important than moisture for the emergence of temperate biome species, and larger seeded species can germinate at a broader range of temperatures than smaller seeded species. June, 2010, was a rainy month (158 mm of rain; the normal is 87 mm), and July was also not drier than usual (precipitation of 97 mm; normal of 89 mm) (Environment and Climate Change Canada, 2013a, 2013c). On the other hand, July was a particularly warm month, with 15 consecutive days of maximum temperatures over 27.5 °C, including an important heat wave (>30 °C) from 5 July to 9 July (Environment and Climate Change Canada, 2013a). Some species, like *Fraxinus excelsior* and *Acer pseudoplatanus*, do not emerge when the daily maximum soil temperature exceeds 25 °C (Jinks *et al.* 2006). Germination of *Acer saccharum* also drops as temperatures increases; it is optimal at 1 °C and does not germinate well at temperatures above 10 °C (Burns and Honkala, 1990). The warm temperatures experienced at the beginning of the first growing season and the late period of seeding (at the end of May instead of late April) may explain the failure of sugar maple emergence, as well as other species.

The heat wave period corresponded with the moment where the five tamarack seedlings emerged and died and the moment where pine seedlings began to slowly perish (Fig. 1.1a). Almost 70% of the pine seedlings died in the first growing season. Then, half of the remaining pine seedlings died during the first winter. Gill and Marks (1991) also observed similar patterns of desiccation and frost heaving on young pine seedlings. The low emergence of pine seedlings in the second experiment may be explained by the alkaline nature of the soil (IRDA, 2008); red pine is known to grow better when the soil has a pH between 5.1 and 5.5 (Burns and Honkala, 1990).

Like our experiment, other studies have obtained a better survival for oak than for pine seedlings (Willoughby *et al.*, 2004; Mendoza *et al.*, 2009). The large nutrient reserves and energy stock in their acorns and their ability to rapidly develop a long taproot presumably allow young oak seedlings to survive short periods of drought or other stresses (Tripathi and Khan, 1990; Burns and Honkala, 1990; Beckage and Clark, 2003; Willoughby *et al.*, 2004).

1.5.2 Effects of Vegetation

No statistically significant effect of vegetation was observed on seedling emergence, survival and height of pine, maple and oak seedlings. Our hypothesis that the emergence of shade tolerant maple seedlings would be enhanced by a vegetation cover was not confirmed. Nonetheless, past studies have shown that an intact vegetation cover may enhance emergence of red maple (*Acer rubrum*) and have a facilitating effect on the survival of sugar maple seedlings (De Steven, 1991a; Berkowitz *et al.*, 1995). Herbaceous vegetation protects shade tolerant *Acer* seedlings from heat and desiccation stresses by providing a shadier environment, with lower light levels and, thus, lower leaf temperatures (Gill and Marks, 1991; Berkowitz *et al.*, 1995).

Some competition for water and light may have occurred, since the diameter and shoot biomass of red oak seedlings were lower and specific leaf area higher when they grew in herb vegetation. On bare soil, where light levels are high, seedlings developed thick leaves (low SLA) to reduce transpiration losses and increase carbon gain (Poorter 1999). Under vegetation, oak seedlings can reduce their leaf biomass to increase their fine root biomass, due to the lack of water in vegetation plots (van Hees 1997). Indeed, we observed, like Löf *et al.* (2004) and Laliberté *et al.* (2008a) did, lower soil water content (SWC) in vegetation plots than in weeded plots. In dry conditions, grassland vegetation considerably reduces soil water, increasing the intensity of competition and, thus, decreasing seedling survival,

whereas in wet conditions, herbaceous vegetation has a smaller effect on seedling survival (Davis *et al.*, 1998, 1999).

The absence of vegetation impact on emergence, survival and height is probably due to the combined effects of variation in the intensity of competition for water and protection by plants from high light levels. In June, 2010, competition for water was probably not a problem, since it was a rainy month (158 mm), and surrounding herb species did not reach their final height. Pine seedling emergence occurred principally at that time when light and soil water content (SWC) were high, even in vegetation plots. Then, in the summer, 2010, competition for water should have been higher, due to the heat wave and warmer conditions, while taller herb plants should have protected seedlings from high light levels.

1.5.3 Effects of Predation

There were no apparent signs of seedling predation on our seedlings, even though predation damage by voles and rabbits were seen on almost 15% of hardwood trees (none on conifers) in the nearby plantation around experimental blocks (St-Denis *et al.*, in preparation). Rodents can be a major cause of seedling mortality in abandoned fields (Gill and Bazzaz, 1991; Ostfield *et al.*, 1997), but the abundance of food probably protected the small seedlings from predation. Seed predation by rodents and birds was not a problem, as no difference in seedling emergence was observed between non-protected and protected sites. Acorns were not predated, even if the study took place in a suburban area, where gray squirrels (*Sciurus carolinensis*) are present, perhaps as the acorns were buried. The absence of acorn predation was also reported by Laliberté *et al.* (2008a) in a similar study. These results do not support our hypothesis regarding a higher predation rate under vegetation cover.

Researchers from the tropics and Australia observed that invertebrates, such as ants, contribute to seed loss (Andersen 1987, Woods and Elliot, 2004; Garcia-Orth and Martinez-Ramos, 2008). Andersen (1987), for example, showed that ants removed 93% of *Eucalyptus baxteri* seeds (seed mass of 0.0019 g) and 58% of *Casuarina pusilla* seeds (seed mass of 0.0022 g) in an Australian woodland. In Mexico, more than 90% of small-seeded (0.0009 g and 0.0068 g), early successional species were predated by invertebrates (Garcia-Orth and Martinez-Ramos, 2008). Ants, beetles, molluscs and microbes are seed consumers, but the first two groups may also transport intact seeds (Hulme and Borelli, 1999; Vander Wall *et al.*, 2005). Predation and/or removal of seeds by ants may have been responsible for the poor success of our small-seeded species. There were many ants in the field, and many ant eggs were observed during weeding. In the plantation around the experimental blocks, more than 10% of the planted trees

growing on a bare soil were surrounded by ant-hills and around 5% for trees growing in vegetation (St-Denis *et al.*, in preparation).

In the tropics, seed predation by ants may be equivalent or higher than seed predation by vertebrates and ants, like leaf-cutter ants, can also attack seeds of medium size (>0.2 g or >5 mm) (Woods and Elliot, 2004; Garcia-Orth and Martinez-Ramos, 2008). However, a study conducted in the UK showed that seed losses attributable to invertebrates were negligible or null when seeds were buried (Hulme and Borelli, 1999). Indeed, other studies indicated that burying seeds reduces seed loss (Garcia-Orth and Martinez-Ramos, 2008; Doust, 2011; Willoughby *et al.*, 2011). The effect of invertebrate predation has rarely been controlled in direct seeding studies, particularly in Canada (see Hulme 1998), and we are an example of a research bias towards protecting from mammal and bird predation of seeds without considering the possible effects of smaller organisms on small-seeded species. We thus encourage future researchers to consider the potential effect of invertebrate predators, such as ants, in seeding experiments.

1.6 Conclusion and Restoration Implications

It is difficult to establish with certainty why small-seeded species did not emerge in the field. A lack of appropriate temperature and soil moisture or ants may have been important factors impeding the emergence of small-seeded species, but further research is required to determine the actual causes. Our results confirm other studies about increasing seedling emergence and survival with increasing seed size. Hooper *et al.* (2002) and Doust *et al.* (2008) also concluded that large-seeded species of medium to high shade tolerance are good candidates for direct seeding, even under a dense vegetation cover. No effects of vegetation and predation were observed in our study on emergence, survival and height growth of red pine, sugar maple and red oak seedlings. Negative effects due to competition were only observed on red oak diameter and shoot biomass. In this study, vegetation control and protection against mammal and bird predation were unnecessary. Red oak and bur oak seem to be promising species for forest restoration of abandoned fields by direct seeding, but other large-seeded species, such as walnut and hickory, should be tested to confirm the potential of using large-seeded species for direct seeding in forest restoration projects.

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CHAPITRE II

2. PREDATION, COMPETITION, AND FACILITATION AFFECT TREE SUCCESS IN ABANDONED FIELDS: THE BASIS FOR PRECISION RESTORATION

Article qui sera soumis à *New Forests*

Annick St-Denis, auteure principale
Centre d'étude de la Forêt, Département des Sciences Biologiques, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, Canada, H3C 3P8.
st-denis.annick.2@courrier.uqam.ca

Christian Messier
Centre d'étude de la Forêt, Département des Sciences Biologiques, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, Canada, H3C 3P8 ; Institut des Sciences de la Forêt Tempérée, Université du Québec en Outaouais, 58 rue Principale, Ripon, Canada, J0V 1V0.
messier.christian@uqam.ca

Daniel Kneeshaw
Centre d'étude de la Forêt, Département des Sciences Biologiques, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, Canada, H3C 3P8.
kneeshaw.daniel@uqam.ca

2.1 Abstract

Tree seedlings planted in abandoned agricultural fields interact with herb communities through competition, tolerance, and facilitation. In addition, they are subject to herbivory by small mammals, deer or invertebrates. To increase forest restoration success of abandoned fields and reduce management costs, it is important to identify which species are tolerant to or facilitated by herbaceous vegetation and which ones require protection from competition, but also predation. Eight native tree species were planted in plots covered by herbaceous vegetation, in plots where herbaceous vegetation was removed, and in plots where seedlings were surronded by an organic mulch mat. Half of the seedlings were protected against small mammal damage. Two non-pioneer and moderately shade-tolerant species were inhibited by herbaceous vegetation. Birch species were particularly affected by small mammal predation. No effects of predation or herbaceous competition were observed for conifer species. Rather, herbaceous vegetation had positive effects on the survival and the height growth of tamarack (*Larix laricina*). None of the tested herb communities had a stronger competitive effect on tree growth than another. Restoration of abandoned fields using multi-tree species should be designed at the seedling scale rather than at the site scale to account for variable site conditions and different tree responses to predation and competition. An approach resembling precision agriculture could be implemented to lower costs and potential negative impacts of more intensive vegetation management interventions.

Key words: Tree plantation, precision restoration, abandoned agricultural field, predation, competition, tolerance, facilitation

2.2 Introduction

Facilitation has been proposed as a possible restoration tool for woody species (Padilla and Pugnaire, 2006; Gómez-Aparicio, 2009). According to the stress-gradient hypothesis (SGH), facilitation occurs principally in dry and stressful environments such as deserts and alpine areas while competition prevails in better environmental conditions (Bertness and Callaway, 1994; Callaway and Walker, 1997; Holmgren *et al.*, 1997; Callaway *et al.*, 2002). It has been observed that the improvement of emergence, survival, growth, or fitness of young trees (facilitation) is mainly induced by nurse shrubs and trees rather than herbaceous neighbours (Callaway, 1997; Gómez-Aparicio, 2009). For instance, dense herbaceous communities colonizing abandoned agricultural fields may inhibit the establishment and growth of many tree species for many years (Niering and Goodwin, 1974; Benjamin *et al.*, 2005). Competition for soil water between tree seedlings and herb species is recognized as a principal factor affecting tree survival and growth, although when water is not limiting, herbaceous vegetation may have no perceptible effect on tree seedlings (tolerance) (De Steven, 1991b; Burton and Bazzaz, 1995; Davis *et al.*, 1998, 1999; Laliberté *et al.*, 2008b). Consistent with the SGH, facilitation effects on growth are generally restricted to less favorable environments (Goldberg *et al.*, 1999). For survival, however, competition may decline with productivity and facilitation may occur in productive systems such as mesic temperate habitats (Goldberg *et al.*, 1999; Gómez-Aparicio, 2009). Indeed, positive effects of herbaceous cover on tree emergence and survival have been previously observed in abandoned temperate fields whereby the presence of herbaceous vegetation reduced frost heaving, heat and desiccation stresses on tree seedlings (De Steven, 1991a, 1991b; Gill and Marks, 1991; Berkowitz *et al.*, 1995).

The relationship between herbaceous plants and tree seedlings is also influenced by the functional characteristics of trees and herbs. Pioneer tree species have a greater proportion of deep roots, higher cumulative root length and number of root apices than non-pioneer species, allowing them to explore larger volumes of soil and to be better adapted to water and nutrient limited sites (Gale and Grigal, 1987; Coll *et al.*, 2008). Moreover, pioneer species can rapidly outgrow the vegetation layer due to their faster growth rates, although their establishment may be limited by herbaceous vegetation, whereas moderately to highly shade-tolerant species establish better under herb cover but grow more slowly (Hooper *et al.*, 2002; Doust *et al.*, 2006, 2008). On the other hand, some herb communities are known to be stronger competitors than others. With their large root / shoot ratio, their clonal growth form, their ability to produce tillers and spread rapidly, grasses are generally greater competitor than forbs (Caldwell and Richards, 1986; Pywell *et al.*, 2003; Gómez-Aparicio, 2009. However, some forb species that form dense communities (*e.g. Solidago* and *Aster* sp.) may compete with tree seedlings or inhibit them via the

production of allelopathic compounds, although allelopathic effects remain mainly hypothetical (Horsley, 1977; Burton and Bazzaz, 1995; de Blois *et al.*, 2004).

In addition to its variable direct effects on different species of tree seedlings, herbaceous vegetation cover has indirect effects on seedlings by increasing rates of small mammal predation by sheltering them from larger predators (Gill and Marks, 1991; Ostfeld and Canham, 1993; Pusenius *et al.*, 2000). Rabbits and voles, but also deer and invertebrates may cause serious damage on tree seedlings, and the importance of herbivory depends on predator density, tree species, seasonality, the presence of a vegetative cover, the size of tree plantation and the distance to woodland (Gill and Marks, 1991; Ostfeld *et al.*, 1997; Stange and Shea, 1998; Moore *et al.*, 1999, 2000; McPherson, 1993).

Due to predation and competition, most tree plantation projects on abandoned fields used protection against predation as well as control of herbaceous vegetation (Ward *et al.*, 2000; Sweeney et al. 2002; Groninger, 2005; Cogliastro *et al.*, 2006). Mechanical control treatments, such as plowing, have been used to reduce herbaceous competition, but they can also slow down site restoration by eliminating natural regeneration, disturbing soil, and decreasing organic matter, microbial activity and mycorrhizal diversity (Sampaio *et al.*, 2007, Barea *et al.*, 1997, Alguacil *et al.*, 2008). Light mechanical treatments, such as mowing and shallow cultivation, have also been used, but their effects fade rapidly (Cogliastro *et al.*, 1990; Coll *et al.*, 2007). Despite their lower efficiency in controlling root competition by herbaceous plants, plastic and weed cloth mulch mats are often privileged as they efficiently decrease aerial competition, have positive effects on tree growth by increasing soil temperature and moisture, and because they are more socially accepted than herbicides (Davies, 1985, 1988; Truax and Gagnon, 1993; Lambert *et al.*, 1994). However, using non-biodegradable mulching materials, or plastic spiral protectors and treeshelters against predation requires returning to the planting site after a few years to remove these materials.

Because tree responses to predation, herbaceous competition or environmental conditions are not the same for every species, restoration of abandoned fields should be designed at the seedling scale rather than the field scale. Treatments should be applied according to variable site conditions and the characteristics of the tree species. This approach is based on the principles of precision agriculture to increase efficiency and decrease environmental and economic costs. Many definitions of precision agriculture have been proposed since its inception in the 1980s, but Gebbers and Adamchuk (2010, p. 828) summarized it as "a way to apply the right treatment in the right place at the right time". We propose that precision restoration requires application of the right treatment to the right species at the right place.

2.2.1 Objectives and hypotheses

In this paper, we pose the following questions: (1) Are different tree species or tree functional groups affected differently by predation and herbaceous competition? (2) Is the growth of different tree species influenced by the abundance of some herb groups and by soil moisture? We hypothesized that: (1) conifer species are less affected by predation than broadleaved species; (2) survival of moderately to highly shade-tolerant species is not negatively affected by herbaceous vegetation, but (3) the growth of these non-pioneer species is more strongly affected by competition than are pioneer species; and (4) competition effects on tree growth increase with the abundance of *Solidago* and *Aster* species that surround tree seedlings. The main goal of this research was to test whether restoration success of abandoned agricultural fields using multi-tree species could be improved by a greater functional understanding, at the tree species level, of the effects of predation, competition and facilitation on tree survival and growth.

2.3 Methods

2.3.1 Study area

The study was conducted in a peri-urban area of Montréal (Québec, Canada), in the agricultural zone of Laval (45°40′N; 73°43′W). The regional climax forest is a sugar maple – hickory forest. The climate is humid continental with average annual temperature of 6.8 °C, recorded at the Montréal Pierre Elliott Trudeau weather station (45°28′N; 73°45′W). Monthly means are 21.2°C in July and –9.7°C in January, the warmest and the coldest month (means were calculated for the 1981–2010 period; Environment and Climate Change Canada, 2013c). Annual precipitation is 1000 mm, of which around 20% falls as snow (Environment and Climate Change Canada, 2013c). The experiment took place in three abandoned agricultural fields. Field #1 (surface area ≈9000 m^2) is separated from field #2 (≈23,000 m^2) by a ditch bordered by eastern cottonwood (*Populus deltoides*) trees. These two fields are situated on the south side of a 3.5 ha forest composed of silver maple (*Acer saccharinum*), black ash (*Fraxinus nigra*), green ash (*Fraxinus pennsylvanica*), eastern cottonwood (*Populus deltoides*) and eastern white cedar (*Thuja occidentalis*) trees. Field #3 (≈9000 m^2) is located on the north side of this forest.

The abandoned fields had similar past land use. They were cultivated for more than 25 years for grains and vegetables until the early 2000s. Following this agricultural period, the sites were colonized by ruderal herbaceous species and were mown once or twice a year, until the fall preceding the experiment

(2009). The vegetation was principally dominated by grass species (*Poaceae* spp. and *Cyperaceae* spp.), *Solidago*, *Trifolium*, *Sonchus* and *Aster* species. *Daucus carota*, *Taraxacum officinale*, *Cirsium* spp., *Arctium* spp. and *Erigeron* spp. were also common. Total ground coverage by all species was around 65% in each field at the time of plantation. Mowing prevented tree and shrub establishment, but ash (*Fraxinus* sp.) seedlings colonized the sites as soon as mowing ceased, *i.e.* in first summer (2010) following plantation.

The surface deposit is a mix of glacial (till) and marine deposits. Soil is an orthic melanic brunisol type (IRDA 2008). The first two fields and the majority of the third one are covered by a stony clay loam that is moderately well drained while the remaining part of the third field is a well-drained clay loam (IRDA 2008). Topography is mainly flat although there are slight depressions. The experimental design (see below) was included in a restoration project of the abandoned fields using more than 15 000 tree and shrub seedlings (height < 1 m) planted from June to August 2010, at least 2 meters from experimental plots.

2.3.2 Experimental design

The study took place between the end of May 2010 and the end of September 2012. Trees were also measured in June 2015, but no vegetation treatment (weeding or mowing) was done between 2012 and 2015. Four 40.5 m × 27 m experimental blocks were established at least 25 metres from mature trees and roads, along an east-west axis: one in field #1 (surface area of ≈ 1 ha), two in the second field (23 ha), and one in field #3 (1 ha). Experimental blocks were divided into six plots following a split-plot design where the main factor was "protection" (plastic spirals against small mammals vs no protection) and the sub-plot factor was "vegetation" (VG, intact herbaceous vegetation; M, mulch mats; BS, bare soil). Eight tree seedlings of eight species were randomly planted within each plot for a total of 192 trees per species. Species that were used in the experiment are native to the area and easily available, and represent a gradient of growth rates and shade tolerances (Table 1). The chosen species were: paper birch (*Betula papyrifera*), yellow birch (*Betula alleghaniensis*), tamarack (*Larix laricina*), red pine (*Pinus resinosa*), northern red oak (*Quercus rubra*), red ash (*Fraxinus pennsylvanica*), red maple (*Acer rubrum*) and sugar maple (*Acer saccharum*).

Container-produced tree seedlings were obtained from the Berthier nursery (Berthierville, QC) of the *ministère des Fôrets, de la Faune et des Parcs du Québec* and were delivered in cold-storage. All tree seedlings were container-produced (initial sizes are provided in table 2.1). Broadleaved species were one-year-old, while conifer species were two-years-old. Seedlings were kept in a dark cool room (≈15°C) until

manual planting from May 28 to June 11, 2010. Seedlings were planted at 1.5 m spacing from one another. They were watered once after planting.

One-third of the tree seedlings were planted directly into the herbaceous vegetation (VG), which was less than 20 cm high at the time of planting. Another third of the tree seedlings were surrounded by a 50 cm × 50 cm × 8–10 mm organic mulch mat (M) made of coconut fiber (Biomat, Multi-formes Inc., La Guadeloupe, QC) installed immediately following planting. Mats were affixed to the ground surface with four U-nails. Finally, the remaining tree seedlings were planted on bare soil (BS). Before planting, herbaceous vegetation was cut to the ground level with a gasoline-powered weed cutter. An herbicide (Roundup® concentrate, glyphosate 143 g/L; 100 mL diluted in two litres of water, 25 L/ha) was applied within a 50 cm radius of the locations in which seedlings were to be planted. Tree seedlings were planted one week after herbicide application. From July 2010 to September 2012, the vegetation was regularly hand-weeded to maintain bare soil conditions in a 30 to 35 cm radius around each tree. In rows between bare soil seedlings, vegetation was mowed with the weed cutter to prevent the herbaceous vegetation from exceeding 20 cm in height.

In July 2010, half of the tree seedlings were protected from small mammals (voles, rabbits, etc.) using spiral plastic protectors (TIMM Enterprises Ltd., Milton, ON) 35 cm high, affixed to the ground with a U-nail. If trees were smaller than 50 cm tall, plastic protectors were cut to adjust to seedling size. Seedlings affected by predation before the installation of the protectors (<2 %) were excluded from the analyses.

Table 2-1 Characteristics of the eight tree species

Common name	Scientific name	Mycorrhizal association	Successional status	Growth rate	Shade tolerance	Initial mean height (cm)	Initial mean diameter (mm)
Tamarack	*Larix laricina* (Du Roi) K. Koch	EM	Pioneer	Rapid	1	38.7	6.8
Red pine	*Pinus resinosa* Aiton	EM	Pioneer	Rapid	1.9	25.9	5.9
Paper birch	*Betula papyrifera* Marsh.	EM	Pioneer	Rapid	1.5	30.1	4.0
Red ash	*Fraxinus pennsylvanica*	AM	Pioneer	Rapid	3.1	33.8	4.8
Red maple	*Acer rubrum* L.	AM	Pioneer	Rapid	3.4	62.3	6.9
Northern red oak	*Quercus rubra* L.	EM	Non-pioneer	Moderate	2.8	41.8	5.7
Yellow birch	*Betula alleghaniensis* Britt.	EM	Non-pioneer	Slow	3.2	37.0	3.8
Sugar maple	*Acer saccharum* Marsh.	AM	Non-pioneer	Slow	4.8	53.0	5.6

AM: arbuscular mycorrhizal species, EM: ectomycorrhizal species; Successional status and growth rate: USDA, NRCS, 2013; Burns and Honkala, 1990; Shade tolerance scales range from 0 (not tolerant) to 5 (maximum tolerance): Niinemets and Valladares, 2006.

2.3.3 Tree measurements

2.3.3.1 Survival and growth

Tree survival was evaluated every spring and fall from fall 2010 to fall 2012 as well as in June 2015. Tree mortality due to small mammal predation can be inferred to be when survival rates are higher for seedlings protected with a plastic spiral than for seedlings unprotected. Direct observations of predation (rabbit, vole or deer predation) damage causing tree mortality were also made. Height and diameter were measured every fall (2010–2012) and in June 2015. Height was measured as the distance between the soil surface and the apical meristem while diameter was measured 5 cm above the soil surface. We calculated the relative growth rate (RGR_X) of height or diameter using this formula:

$$RGR_X = \frac{\ln(X2) - \ln(X1)}{T2 - T1}$$

where X1 corresponds to seedling height or diameter in year T1, X2, height or diameter in year T2.

2.3.3.2 Foliar measurements

Foliar predation by invertebrates and foliar pathogens were estimated for all tree seedlings in September 2011. When more than 30% of leaves showed signs of invertebrate predation (such as sawfly damage) or disease (such as tar spot of maple), we classified the seedling as being affected by invertebrate predation or foliar disease. The number of leaves or branches (for conifers) was counted on each seedling between the end of July and the beginning of August 2012. Between August 15–23 2012, two trees per species were randomly chosen in each plot among those having a minimum of 25 leaves (if not possible, trees having the highest number of leaves were chosen). This minimum number of leaves per individual was required for foliar analyses. Leaves and needles were placed between wet paper towels and were kept moist and cool until laboratory analysis. Specific leaf area (SLA) was only measured for leaves of the hardwood species: paper birch, red maple, yellow birch, red oak and sugar maple. SLA was measured following the method described by Cornelissen *et al.* (2003). Ten healthy leaves, or the maximum number of healthy leaves if there were less than ten leaves, were scanned the day of collection. Leaf area was calculated using the Winfolia software (Régent Instruments, Québec, Canada). All leaves and needles were dried at 70° C for at least 48 hours before their mass was measured or before grinding. SLA was calculated as the total one-sided area of fresh leaves divided by their oven-dried mass and was expressed in $mm^2\ mg^{-1}$. Leaves were finely ground with a vibratory pulverisette (Fritsch, Idar-Oberstein, Germany). Between each sample, the pulverisette was cleaned with a vacuum and rinsed with ethanol (70%).

Concentrations of nitrogen (leaf N) were analysed on a Leco CNS−2000 (LECO, St-Joseph, USA) by the laboratory of the Canadian Forest Service's Laurentian Forestry Centre.

2.3.4 Environmental variables

2.3.4.1 Soil water content (SWC) and light

Environmental measurements were taken on two seedlings per species that were randomly selected in each plot. Soil water content (SWC) was measured three times in the summer 2011 with a TDR-200 probe (Spectrum Technologies Inc., Plainfield, IL, USA), using 12 cm rods. The first measurements were taken on June 10th, two days after a 10 mm rain, but the 9 preceding days were without rain (Environment and Climate Change Canada, 2013a). The second measurements were taken on 17 August, one day after a 11 mm rain and three days after a rain of 22 mm. The third measurements were taken on 23 August, one day after a 3 mm rain and 2 days after a 40 mm rain (Environment and Climate Change Canada, 2013a). SWC was also estimated on 21 September 2012, three days after a 21 mm rain (Environment and Climate Change Canada, 2013b). Photosynthetic photon flux density (%PPFD) was measured using point quantum sensors (LI-COR Inc., Lincoln, USA) at a height of 30 cm on the south side of the seedling. Measurements were taken at the end of July, 2011, on cloudy days, following the method described in Messier and Puttonen (1995).

2.3.4.2 Herbaceous vegetation

On 17 August 2011, herbaceous biomass was measured around one randomly chosen seedling per species in each VG and M plot. After the first year, some herb plants began to pierce the organic mulch mats or grew through the crack in the middle of the mulch mats. All plants inside a 50 × 25 cm plot installed on the east side of the selected seedling were cut to ground level and placed in a paper bag. Samples were air dried at 25° C until there was no further loss of mass due to humidity and then weighed to estimate above-ground biomass of the surrounding vegetation. On 23 July 2012, in VG plots, an inventory of herbaceous vegetation was made next to the two same seedlings randomly chosen for SWC. All herbaceous species in a 50 × 25 cm plot were identified and their percent cover was evaluated. We grouped the species into five herb communities: Graminoids (grasses), *Solidago* spp. such as *Solidago rugosa*, *Asteraceae* spp. such as *Sonchus arvensis*, *Fabaceae* species (legumes) such as *Trifolium repens*, and *Apiaceae* mainly dominated by *Daucus carota*. More than 95% of the species identified fit into these groups. Mean height of the surrounding herbaceous vegetation was estimated at the same time.

2.3.5 Statistical analysis

Seedling survival was evaluated using Chi-squared tests. We first compared survival rates between experimental factors (protection, vegetation and protection x vegetation) from fall 2010 to fall 2012 and, in the spring of 2015. We then compared mortality rates due to predation by small mammals (data combined from 2010 to 2012) between the vegetation treatments. Repeated measures analyses of variance (ANOVAR) and univariate analyses of variance (ANOVA), based on the two-way split-plot design, were performed for each species to evaluate the effects of protection and vegetation treatments on seedling height and diameter, number of leaves or conifer branches, leaf N, SLA, and SWC. Herbaceous biomass and light (%PPFD) were only compared between VEGETATION and MULCH MAT plots with ANOVAs. Student and Tukey tests were used as *post-hoc* tests. Log transformations were used when data were not normal. A multiple regression was used to estimate the effects of SWC, average herbaceous cover height, and percentage cover of each herb community on the height and diameter relative growth rate (RGR) of each tree species. All statistical analyses were performed using JMP 10.0 and statistical significance was determined at $p = 0.05$.

2.4 Results

2.4.1 General

With the exception of paper birch, seedlings of the pioneer species exhibited greater survival than did non-pioneer species. After five seasons of growth, mortality rates varied from 3% for red ash seedlings to 61% for yellow birch seedlings, all treatments combined (Fig. 2.1). Pioneer species such as tamarack, paper birch, and red ash were the species with the highest height and diameter increments between fall of 2010 and spring of 2015 whereas the non-pioneer species red oak had the lowest growth (Fig. 2.2).

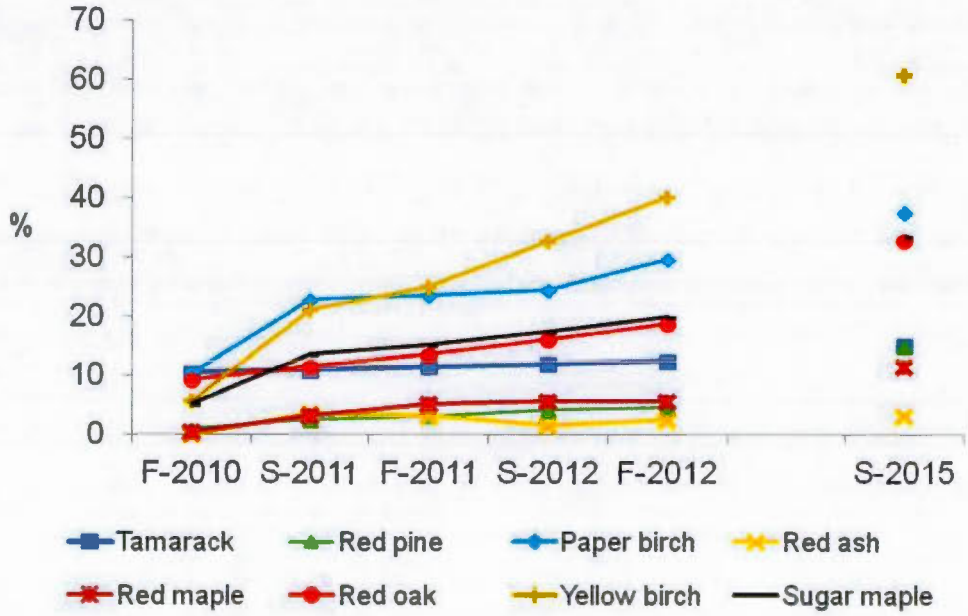


Figure 2-1 Rates of seedling mortality in function of tree species from fall 2010, spring and fall 2011, spring and fall 2012, and spring 2015.

2.4.2 Effects of predation and herbaceous vegetation on tree survival and growth

Mortality due to predation was generally higher for non-pioneer species than for pioneer species, with the exception of paper birch (Tables 2.2 and 2.3). In fact, both birch species had mortality rates double that of the next most vulnerable species (Fig. 2.1, Table 2.3). Many birch seedlings were found dead after the first winter and their mortality was principally related to predation, although competition also affected yellow birch survival (Fig. 2.1, Table 2.2). Yellow birch (17%), paper birch (15%), red oak (7%) and sugar maple (6%) seedlings showed more signs of lethal small mammal damage than other species (Table 2.3). The vegetation control treatments also had an important impact on predation rates in the most vulnerable species. Seedlings of both species in the birch genus surrounded by mulch mat (M) were more affected by small mammal damage than seedlings growing in vegetation (VG) (Table 2.3; $\chi^2 = 23.153$, $p = <0.0001$). However, birch seedlings in both of these treatments were more susceptible to predation than bare soil (BS) seedlings ($\chi^2 = 15.634$, $p = 0.0004$). The mortality due to predation of the non-pioneer species, red oak and sugar maple, was also inferior or did not occur in BS plots (Table 2.3; $\chi^2 = 11.544$, $p = 0.0031$; $\chi^2 = 10.050$, $p = 0.0066$, respectively). Effects of predation on red maple were observed in the spring 2015 survey (Table 2.2; $\chi^2 = 8.202$, $p = 0.0042$), but between 2010 and 2012 only 2%

of dead seedlings showed small mammal damage (Table 2.3). Some red ash seedlings (3%) snipped by rabbits or voles produced new stems the year following predation, explaining the decrease in mortality rates in 2012 (Fig. 2.1).

The use of plastic spiral protectors did not have much influence on tree growth with the exception of a positive effect on red oak height from the second growing season onward ($p < 0.03$). However, it promoted anthills. In the fall of 2012, 9% of protected seedlings had an anthill inside the protector while less than 2% of unprotected seedlings were surrounded by an anthill ($\chi^2 = 69.217$ $p < 0.0001$). Anthills did not affect tree survival or growth.

Predation by rabbits led to two times more seedling mortality than predation by voles. Both species of birch seedlings were most affected by rabbit predation while red oak was the species preferred by voles (data not shown). Mortality due to small mammal damage was observed on some protected seedlings of yellow birch (5.5%), paper birch (2%) and red oak (1%). For these individuals, voles were observed to have cut roots under the spiral protector while rabbits cut the stem above the protector. Herbivory by deer was negligible, only 5 seedlings died due to deer predation. Foliar herbivory by invertebrates was also minor (4% of tree seedlings, in total) and did not vary between treatments. Conifer species were not affected by any kind of herbivory.

Tree height and tree diameter responded similarly to vegetation treatments than tree diameter (Fig. 2.2). In general, the survival of the pioneer species was not negatively affected by herbaceous vegetation except at the end of the experiment for paper birch and red maple seedlings (Table 2.2). However, the growth of broadleaved pioneer species was usually higher in bare soil plots (Fig. 2.2). The conifer species were either tolerant of or facilitated by the presence of the vegetation layer. Red pine survival (>95% within the first 3 years), height, and diameter did not vary with any treatment at any time (Table 2.2, Fig.2.2b). Mortality of tamarack seedlings occurred principally within the first growing season following planting in bare soil plots or in mulch mat plots (Fig. 2.1a, Table 2.2). No effects of herbaceous vegetation were observed on tamarack diameter, but tamarack seedlings growing in BS plots were smaller than those in M or in VG plots, after the first ($F = 9.7673$; $p = 0.0118$) and the second ($F = 13.4052$; $p = 0.0061$) growing seasons (Fig. 2.2a). After three years, this relation was only marginally significant ($p = 0.0922$) and it was not significant in the spring of 2015 ($p = 0.4503$).

Table 2-2 Predation, competition, and facilitation effects on tree seedling survival from fall of 2010 to spring of 2015

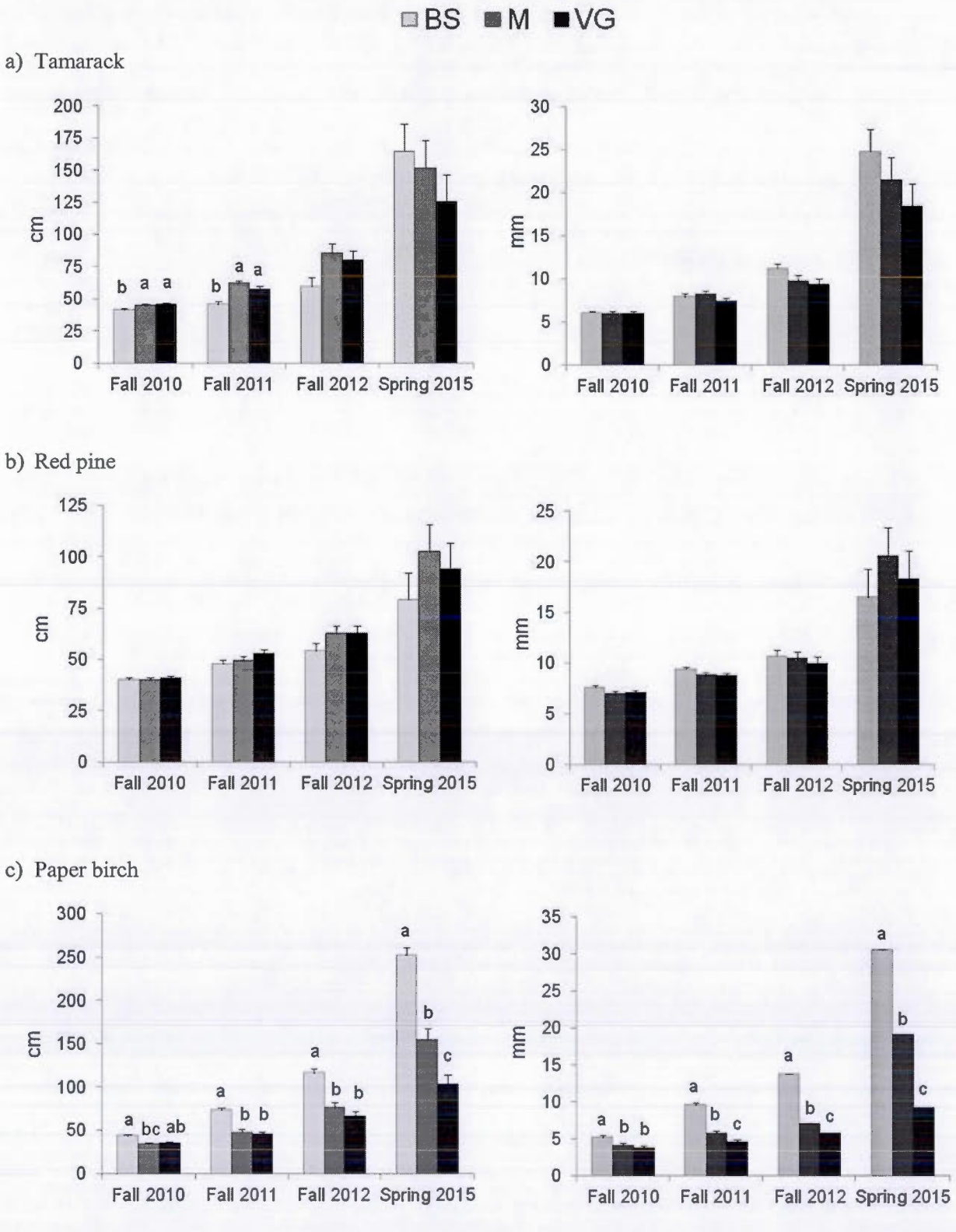
Species	Factor	Fall 2010	Spring 2011	Fall 2011	Spring 2012	Fall 2012	Spring 2015
Tamarack	Protection Vegetation	Facilitation *	Facilitation *	Facilitation *	Facilitation *	Facilitation **	Facilitation **
Red pine	Protection Vegetation						
Paper birch	Protection Vegetation		Predation in VG*		Predation **	Predation ** M < BS = VG*	Competition ***
Red ash	Protection Vegetation						
Red maple	Protection Vegetation						Predation ** Competition **
Red oak	Protection Vegetation	Predation **	Competition **	Competition **	Predation ** Competition ***	Predation ** Competition ***	Competition ***
Yellow birch	Protection Vegetation		Predation *** Competition **	Predation *** Competition **	Predation *** Competition **	Predation *** Competition ***	Competition ***
Sugar maple	Protection Vegetation	Facilitation *		Predation in VG* Facilitation if Protection * M < BS = VG if No Protection*	M < BS = VG *		M < BS = VG **

BS: tree seedlings growing in bare soil plots, M: surrounded by organic mulch mat, VG: or in intact herbaceous vegetation. Blank spaces mean survival did not differ between treatments. Predation means survival was lower for seedlings unprotected against small mammals. Competition means survival is higher when trees are growing in bare soil (BS > M = VG or BS > VG > M). Facilitation means survival is higher when trees are growing in herbaceous vegetation (BS = M < VG or BS < M = VG). *P*-value: * <0.05; ** < 0.01; *** < 0.001

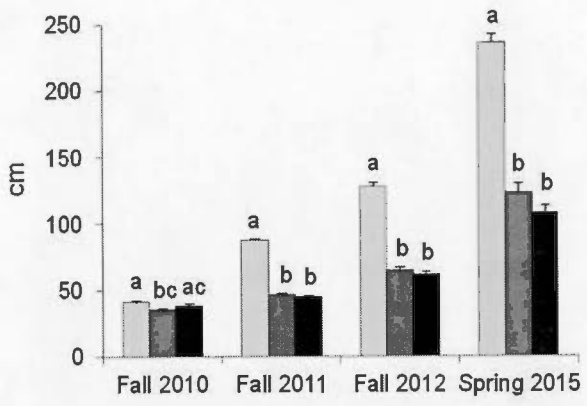
Table 2-3 Tree mortality (%) due to predation compared between vegetation treatments (evaluated using signs of lethal small mammal damage on unprotected and protected seedlings, data compiled from Spring 2010 to Autumn 2012), tree mortality in Autumn 2012 compared between protection treatments, and tree mortality in Spring 2015 (total)

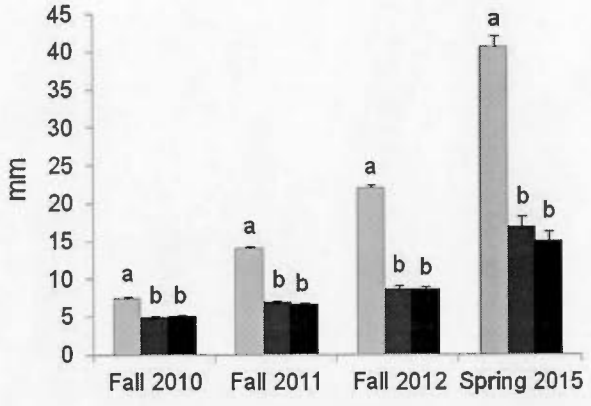
Species	Mortality due to predation (2010-2012)				% dead seedlings (Fall 2012)			% total dead seedlings (Spring 2015)
	BS	M	VG	Total	Unprotected	Protected	Total	
Tamarack	0	0	0	0	6.8	5.8	12.6	15.2
Red pine	0	0	0	0	0.5	4.2	4.7	15.1
Paper birch	1.1 a	8.9 b	4.7 c	14.7	20.4 a	9.4 b	29.8	37.7
Red ash	0	2.1	0	2.1	2.1	0.5	2.6	3.1
Red maple	0	0.5	1.6	2.1	4.2	1.6	5.8	11.5
Red oak	0 a	2.6 b	4.2 b	6.8	13.6 a	5.2 b	18.8	33.2
Yellow birch	0.5 a	10.1 b	6.4 c	17.0	27.5 a	12.7 b	40.2	60.8
Sugar maple	0 a	3.7 b	2.1 b	5.8	12.1	7.9	20.0	33.5

BS: seedlings growing in a bare soil, M: surrounded by organic mulch mat, VG: or in intact herbaceous vegetation. Means for each species were tested using ANOVA and then compared using Tukey tests following ANOVA. Means of each row followed by different letters are significantly different at $p < 0.05$.

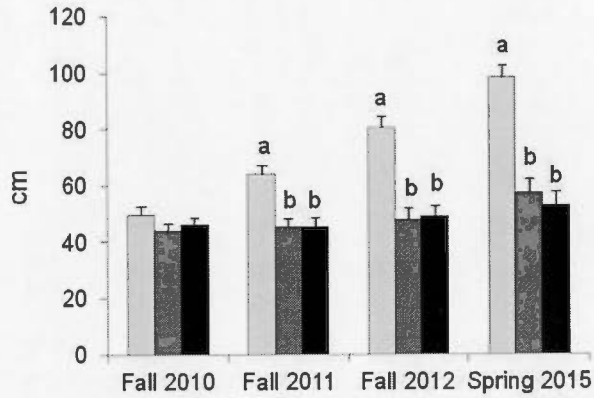

BS M VG
a) Tamarack
cm
mm
Fall 2010
Fall 2011
Fall 2012
Spring 2015
b) Red pine
c) Paper birch

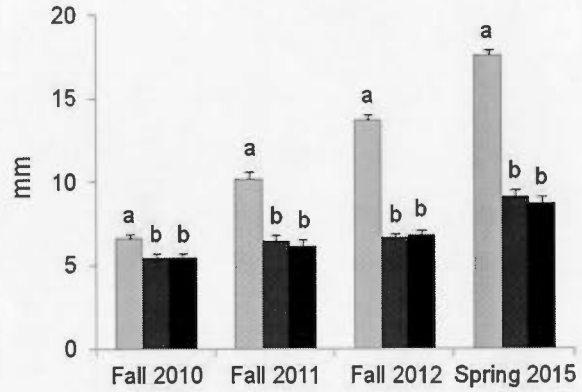
d) Red ash



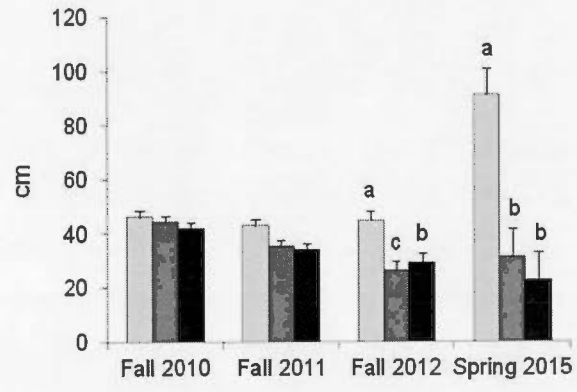


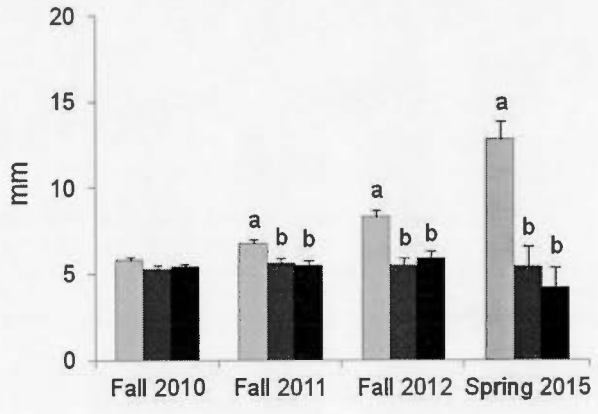
e) Red maple



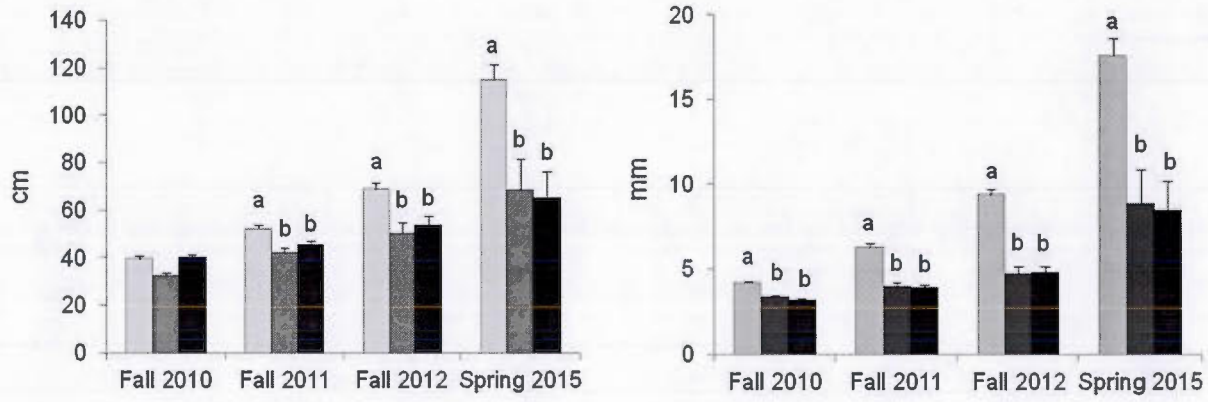


f) Red oak





g) Yellow birch



h) Sugar maple

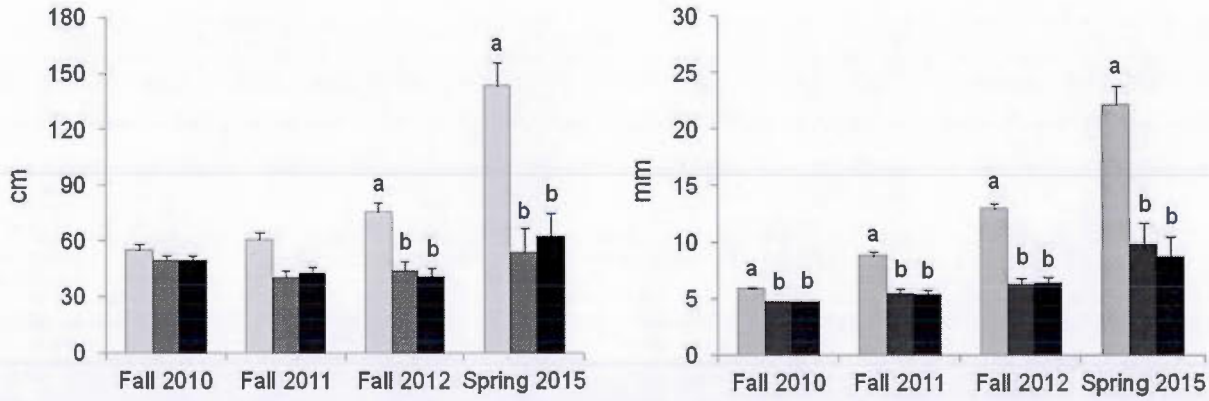


Figure 2-2 Height and diameter of seedlings (least-squares means and SE) growing in bare soil plots (light grey), surrounded by mulch mat (medium grey) or in vegetation plots (black), from autumn 2010–2012 and in spring 2015.

Herbaceous vegetation showed also some evidence of facilitation on sugar maple survival (Table 2.2). After the first growing season, sugar maple survival was lower in BS plots ($\chi^2 = 6.330$, $p = 0.0422$) whereas after the second growing season, sugar maple survival was higher in VG, but only for seedlings protected against predation ($\chi^2 = 6.344$, $p = 0.0419$). The survival of the other two non-pioneer species was on the contrary higher in BS plots (Table 2.2). The growth of non-pioneer species was greater in BS plots (Fig. 2.2).

No benefit of the organic mulch mats on tree survival was observed in this experiment. Mulch mats had comparable effects to or more negative effects than herbaceous vegetation (Table 2.2, Fig. 2.2). In the second growing season, herb biomass (47 g) crossing the organic mulch mats ($F = 2.7507$, $p = 0.1958$) and %PPFD at 30 cm high (60%; $F = 0.7491$, $p = 0.4504$) were not different from herb biomass and %PPFD in intact vegetation (65 g and 69%, respectively). By the end of the experiment, mulch mats were mostly decomposed.

After five years, survival of all pioneer species seedlings growing in herbaceous vegetation was higher than 75 %, except for paper birch (Fig. 2.3a). Excluding red maple, they all had height growth increment of more than 30 cm (Fig. 2.3b). In contrast, non-pioneer species seedlings surrounded by vegetation had lower survival and height growth rate. The size of unprotected red oak seedlings significantly decreased due to leader mortality or the appearance of a new stem following small mammal damage. In fact, this decline in size was observed on more than 50 % of red oak seedlings when all treatments were combined.

2.4.3 Foliar attributes, soil water content, and the influence of herb communities

All broadleaved species but yellow birch had more leaves ($p < 0.01$) and a lower specific leaf area (SLA) ($p < 0.03$) in bare soil plots (SLA was not measured for red ash and conifers). Nitrogen (N) in conifer needles or in birch leaves was not affected by the presence or absence of herbaceous vegetation (Table 2.5). Leaf N was however higher in BS plots for the three endomycorrhizal (AM) tree species: red ash ($F = 47.9526$; $p = 0.0002$), red maple ($F = 11.8862$; $p = 0.0081$) and sugar maple ($F = 55.9883$; $p = 0.0001$). More seedlings with superficial bare roots were observed in BS plots for all species, but paper birch and sugar maple (Table 2.4).

Soil water content (SWC) did not vary between vegetation treatments in 2011 nor in 2012. Further, it did not influence the relative growth rate (RGR) of seedlings growing in herbaceous vegetation (Table 2.5). The relative growth rate (RGR) of red maple and conifer species was positively related to the height of the herbaceous layer. In general, no specific herb community influenced tree growth, other than *Solidago* species which had negative effects on red ash and red maple growth (Table 2.5). Grasses had a marginally significant positive effect ($p < 0.10$) on tamarack growth (Table 2.5).

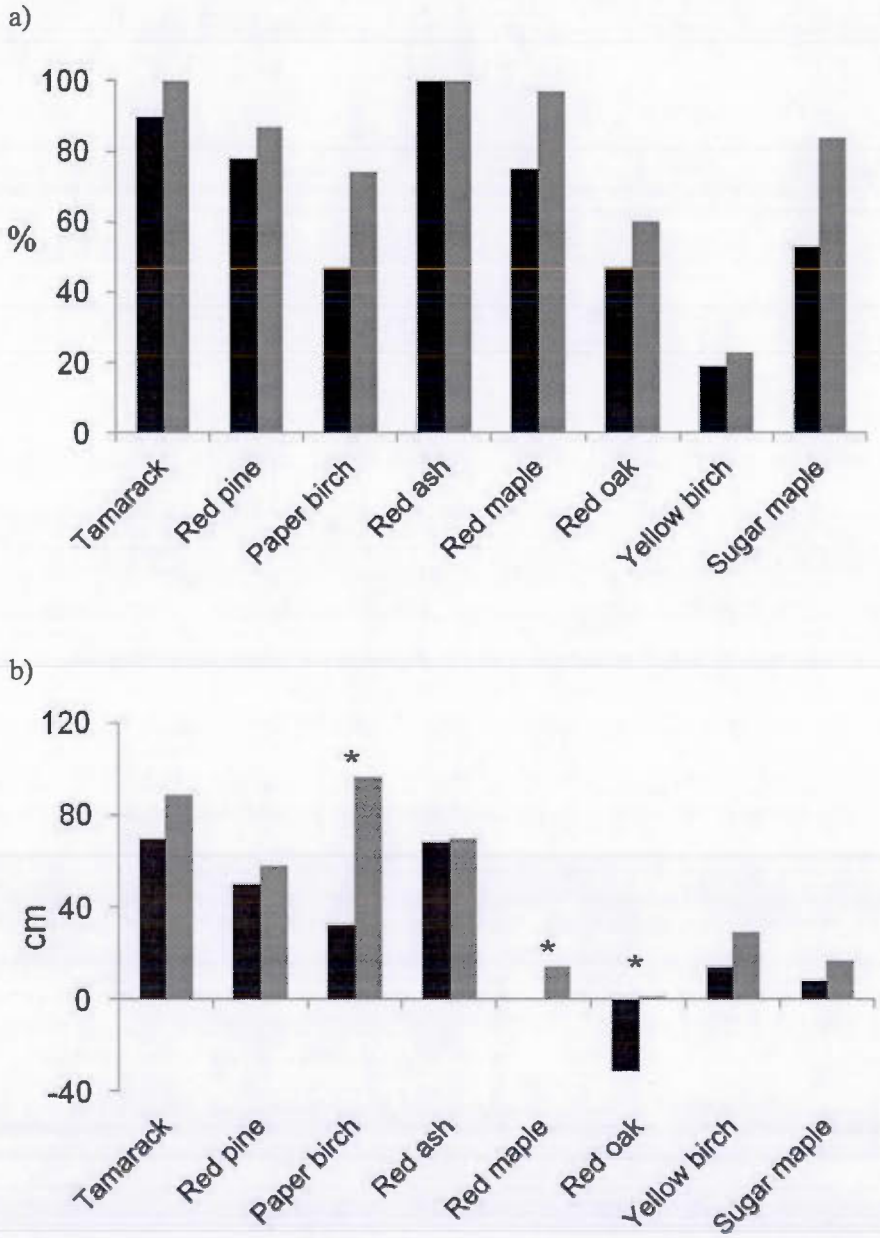


Figure 2-3 Differences of (a) survival rates in spring 2015 and (b) height growth increment (2010-2015) for seedlings growing in herbaceous vegetation. Black bars: seedlings unprotected against small mammal predation. Grey bars: seedlings protected. (* $P < 0.05$, two-sample t-test).

Table 2-4 Vegetation treatment effects on leaf nitrogen (N) and rooting (%)

Species	Leaf nitrogen (N)			Superficial bare roots		
	BS	M	VG	BS	M	VG
Tamarack	1.91	1.46	1.43	11.6 x	1.7 y	2.3 y
Red pine	1.02	1.07	0.97	12.8 x	1.1 y	2.7 z
Red ash	2.30 a	1.43 b	1.62 b	8.1 x	0 y	3.8 z
Paper birch	2.28	1.84	1.93	3.4	0.7	0.7
Red maple	1.68 a	1.16 b	1.23 b	10.4 x	0.6 y	2.7 y
Yellow birch	1.95	1.86	1.79	6.1 x	0 y	0 y
Red oak	1.68 a	1.11 b	1.24 ab	9.2 x	0.6 y	1.8 y
Sugar maple	1.68 a	1.13 b	1.22 b	1.8	0	2.4

For each variable, means of each row followed by different letters are significantly different at $p < 0.02$.

Table 2-5 Results of multiple regressions of height and diameter relative growth rates (RGR) (fall 2012 – fall 2010) in relation to soil water content, average herb height, percentage cover of Grasses, *Solidago*, *Asteraceae*, *Apiaceae*, and *Fabaceae* (legumes) species

Species		Adjusted R^2	Soil water content	Herb height	Grasses	*Solidago* spp.	*Asteraceae* spp.	*Apiaceae* spp.	*Fabaceae* spp.
Tamarack	RGR_{Height}	0.30		***0.03 (+)***	*0.09* (+)			*0.09* (−)	
	$RGR_{Diameter}$	0.28		***0.01 (+)***	*0.08* (+)				***0.03 (+)***
Red pine	RGR_{Height}	***0.39***		*0.06* (+)					
	$RGR_{Diameter}$	0.14		***0.02 (+)***					
Paper birch	RGR_{Height}	−0.07							
	$RGR_{Diameter}$	−0.13							
Red ash	RGR_{Height}	0.11							
	$RGR_{Diameter}$	0.20				***0.02 (−)***			
Red maple	RGR_{Height}	***0.36***		***0.004 (+)***		***0.04 (−)***			
	$RGR_{Diameter}$	0.31		***0.02 (+)***		*0.09* (−)			
Red oak	RGR_{Height}	***0.40***					***0.04 (−)***		***0.02 (−)***
	$RGR_{Diameter}$	−0.05							
Yellow birch	RGR_{Height}	0.03							
	$RGR_{Diameter}$	−0.26							
Sugar maple	RGR_{Height}	−0.16							
	$RGR_{Diameter}$	−0.11							

Only significant effects ($P < 0.05$), in bold and italic, and marginal effects ($P < 0.10$), in italic, are presented. Positive (+) or negative (−) effects.

2.5 Discussion

Generally, tree survival was less negatively affected by herbaceous vegetation than tree growth (Table 2.2, Fig 2.2) and tree mortality was more due to predation than competition effects (Table 2.3).

2.5.1 Predation

Compared to other studies, predation by deer and small mammals was relatively low, supporting that predation is determined by the environment and predator densities (Ostfeld *et al.*, 1997; Stange and Shea, 1998; Sweeney *et al.*, 2002; Bergman *et al.*, 2005). Tree species preferences also differed. For instance, rabbits and voles can potentially inflect damage on pine seedlings in fields or forests (Bucyanayandi *et al,*. 1990; Gill and Marks, 1991; Bergman *et al.*, 2005), but none of our conifer species exhibited any signs of herbivory. Differences in seedling size, growth rate, density of resin droplets on the stem, the presence of specific monoterpenes in the bark, and palatability are among the factors that have been proposed to explain species and seedling preferences of herbivores (Bucyanayandi *et al.*, 1990; Ostfeld *et al.*, 1997; Pusenius *et al.*, 2001). Birch species were the most vulnerable to small mammal damage, particularly by rabbits. They were also the smallest at time of planting (Table 2.1) and had the smallest diameters, at least in the first two years of growth (Fig.1). By the fifth year of growth, red maple was the only species that had been affected by predation and, at that time, one of the species with the smallest diameters (Table 2.2, Fig. 2.2). Our results thus lead us to suggest that seedlings with small diameters are more vulnerable to small mammal damage.

Predation was as important as or more important under mulch mats than in the vegetation layer. Mulch mats may offer the same protective benefits for small mammals against their predators as does an herbaceous cover. They allow voles to feed and move safely beneath cover, whereas the presence of mats may focus attacks made by rabbits by making the young tree seedlings easier to see (apparent) in the vegetation cover.

2.5.2 Competition, tolerance, and facilitation

Contrary to what we expected to see and to what has been observed in the tropics (Hooper et al. 2002, Doust *et al.*, 2006, 2008), the survival of the two moderately shade-tolerant and non-pioneer species was negatively affected by herbaceous competition. In contrast, slight effects of facilitation were identified on the survival sugar maple, the species with the highest shade-tolerance (Niinemets and Valladares, 2006), and consistent with what Berkowitz *et al.* (1995) had observed. Survival and growth of conifer species were not affected negatively by herbaceous vegetation (tolerance), with positive effects also being observed regarding

survival and height growth of tamarack seedlings. These positive effects suggest that facilitation does not only occur in harsh conditions such as dry environments (Bertness and Callaway, 1994; Holmgren *et al.*, 1997; Callaway and Walker, 1997).

Competition for water was probably low on our sites. No effects of soil water content (SWC) on relative growth rates were found for any species and no differences on SWC were observed among treatments. However, herbaceous vegetation may have reduced heat and desiccation stresses in the uppermost few centimetres of soil; reductions that benefited tamarack, which has a shallow root system (Strong and Roi, 1983). In the first two growing seasons, few heat wave (>30 °C) events were observed (Environment and Climate Change Canada, 2013b). Tamarack is one of the species (together with red pine) that has low specific root length (SRL) (Tobner *et al.*, 2013). It develops roots that were shorter and thicker than any of the broadleaved species that were tested. Positive effects of herbaceous vegetation on tree survival have been previously observed in other mesic habitats, including facilitation of pine seedlings in temperate-zone old fields, but facilitation effects on growth such as those that were observed for tamarack are rare (De Steven, 1991b; Gil and Marks, 1991; Goldberg *et al.*, 1999; Gómez-Aparicio 2009). Similarly, the seedling heights of hybrid larch (*Larix* x *marschlinsii* Coaz) that had been planted for a boreal reforestation project were positively related to vegetation cover (Buitrago *et al.*, 2014).

While the growth of broadleaved species was influenced by competition, only endomycorrhizal (AM) tree species had higher leaf N in bare soil plots. Furthermore, *Solidago* species exerted negative effects on red maple and red ash growth. Burton and Bazzaz (1995) also observed lower foliar N for ash seedlings that were growing in *Solidago* patches. In abandoned agricultural fields, forbs and many grass species decrease the rate of N accumulation in the soil (Knops and Tilman, 2000). Frequent mowing promoted *Trifolium* species in the mowing rows in the bare soil plots, from the second growing season onward, which could have a fertilization effect because legumes increase soil N availability (Knops and Tilman 2000). The explanation may be also related to mycorrhizae. Arbuscular mycorrhizal fungi do not promote tree N acquisition at low N supplies, in contrast to ectomycorrhizal fungi (Reynolds *et al.*, 2005; Smith and Read, 2008). Despite the few negative effects of *Solidago* species on tree growth, no herb community seemed to be a stronger competitor than another. The vegetation surrounding the tree seedlings was composed of multiple herbaceous species which may have diluted any allelopathic effects that might occur in pure dense communities of *Solidago* and *Asteraceae* (Horsley, 1977; Burton and Bazzaz, 1995).

We established that conifer species and red ash are tolerant to herbaceous vegetation because they had high survival (>75%) and height increment of more than 50 cm after five years in vegetation plots.

Tree species can be stated as tolerant to herbaceous vegetation if they have high survival rates, even if they have reduced growth, because many of the seedlings will eventually outgrow the vegetation layer (Connel and Slatyer, 1977; De Steven, 1991b). As expected, pioneer species had higher growth rate than non-pioneer species, except for the moderately shade-tolerant red maple which had however a survival rate higher than 75%. Due to a low survival rate (19% for yellow birch) and a low or negative growth rate (for red oak), we consider the two moderately shade-tolerant and non-pioneer species as being inhibited by the herb cover which had both direct and indirect (via predation) effects (Fig. 2.3).

2.6 Toward precision restoration

In this restoration experiment of an abandoned mesic field using multi-tree species as seedlings, soil water content did not differ between treatments and did not affect tree growth. In addition, the abundance of different herbaceous groups did not have much influence on relative growth rates. However, seedling performance varied according to functional groups of trees. In the context of precision restoration, the right treatment should be applied to the right species. For instance, our study showed that conifer species could be planted without controlling for competition and predation, as they were highly tolerant to or facilitated by herbaceous vegetation and unaffected by herbivory. Nevertheless, herbivory may vary with the environment, predator density and the diversity of species used.

CHAPITRE III

3. SPECIES-SPECIFIC RESPONSES TO FOREST SOIL INOCULUM IN PLANTED TREES IN AN ABANDONED AGRICULTURAL FIELD

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Annick St-Denis, auteure principale
Centre d'étude de la Forêt, Département des Sciences Biologiques, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, Canada, H3C 3P8.
st-denis.annick.2@courrier.uqam.ca

Daniel Kneeshaw
Centre d'étude de la Forêt, Département des Sciences Biologiques, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, Canada, H3C 3P8.
kneeshaw.daniel@uqam.ca

Nicolas Bélanger
Centre d'étude de la Forêt, UER Science et Technologie, TELUQ, Université du Québec, 500 rue Saint-Denis, Montréal, Canada, H2S 3L5.
nicolas.belanger@teluq.ca

Suzanne Simard
Department of Forest Sciences, University of British Columbia, 2424 Main Mall, Vancouver, BC, Canada, V6T 1Z4.
suzanne.simard@ubc.ca

Isabelle Laforest-Lapointe
Centre d'étude de la Forêt, Département des Sciences Biologiques, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, Canada, H3C 3P8.
isabelle.laforest.lapointe@gmail.com

Christian Messier
Centre d'étude de la Forêt, Département des Sciences Biologiques, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, Canada, H3C 3P8 ; Institut des Sciences de la Forêt Tempérée, Université du Québec en Outaouais, 58 rue Principale, Ripon, Canada, J0V 1V0.
messier.christian@uqam.ca

3.1 Summary

Tree plantations are commonly used to restore abandoned agricultural fields with varying degrees of success. Agricultural soils differ from forest soils in nutrient availability and microbial communities. The objective of this study was to test the effect of adding small amounts of forest soil on the survival, growth and rates of mycorrhizal fungal colonization of trees planted in an abandoned agricultural field over the crucial first three growing seasons. Seedlings of two arbuscular mycorrhizal (AM) and two ectomycorrhizal (EM) tree species were planted in an abandoned agricultural field. Soil inocula were taken from four forest stands, each dominated by one of the planted species. Half of the soil samples were sterilized before inoculation to distinguish microbial from nutrient effects. The effect of soil inoculum quantity added was tested using 300 and 1500 ml of forest soil. Tree mortality was low and did not vary between treatments. The growth of EM tree species responded, positively or negatively, to forest soil inoculation. A negative feedback was detected on the growth of red oak seedlings inoculated with non-sterilized red oak soil, suggesting support for the Janzen-Connell hypothesis. Seedlings inoculated with EM sterilized soils were smaller than control seedlings, presumably due to lower nutrient availability of EM forest soils compared to agricultural field soil. The majority of the effects, either positive or negative, were observed the first year. After three seasons of growth, only yellow birch seedlings that had received 1500 ml of non-sterilized red oak soil still benefited from soil inoculation. More research is needed in nutrient-limited soils to determine whether inoculation would have greater or longer term benefits on tree survival and growth.

Keywords Abandoned agricultural field, ecological restoration, forest soil inoculation, tree seedlings, tree growth, mycorrhizae.

3.2 Introduction

Long-term intensive agricultural activities may decrease soil organic carbon, nutrient availability as well as microbial biomass (Dick, 1992; Lal, 2004; Rosenzweig *et al.*, 2016). A reduction in mycorrhizal diversity and mycelium abundance has also been reported in such sites (Jonhson, 1993; Helgason *et al.*, 1998; Alguacil *et al.*, 2008). It has recently been suggested that soil microbial communities could be manipulated to enhance the success of ecological restoration (Heneghan *et al.*, 2008; Harris, 2009; Hoeksema *et al.*, 2010). Mycorrhizal fungal and bacterial inoculations have been previously tested to improve the survival and growth of outplanted nursery-produced tree seedlings (Trappe, 1977; Kropp and Langlois, 1990; Torrey, 1992). However, plant response (e.g. biomass) to inoculation could be greater if instead of using a single mycorrhizal fungus, several mycorrhizal fungal species and non-mycorrhizal microbes are present in the inoculum, or the whole–community soil is used as an inoculum (Hoeksema *et al.*, 2010; Urgiles *et al.*, 2014). In effect, mycorrhizal function and behaviour are generally stimulated by an array of soil organisms, although some inhibitory interactions are possible (Fitter and Garbaye, 1994).

A simple method to inoculate trees would be to add soil containing desirable mycorrhizal fungal spores to a site that is deficient in these fungi (Schwartz *et al.*, 2006), such as forest vs agricultural soils. Diversities of arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi are higher in forest soils than in agricultural soils, but AM fungi are more abundant than EM fungi in agricultural soils (Helgason *et al.*, 1998; Berman and Bledsoe, 1998; Dickie and Reich, 2005). Moreover, soils with high carbon levels and well-balanced nutrients generally have a positive impact on tree nutrition (Pinno *et al.*, 2010; Ens *et al.*, 2013). Therefore, adding a small amount of forest soil to an abandoned agricultural field could potentially create planting microsites that optimize tree survival and growth.

Most studies exploring the effects of forest soil inoculum on tree seedlings have used pot studies and/or have conducted short-term (< 1 year) experiments (Packer and Clay, 2000; O'Brien *et al.*, 2011; Urgiles *et al.*, 2014; Dulmer *et al.*, 2014). In pot studies, effects of forest soil transfer were observed on seedling growth, but the soil inoculum was mixed with a

sterilized substrate (Borchers and Perry, 1990; O'Brien, Gomola and Horton, 2011; Urgiles *et al.*, 2014). Thus, tree seedlings had access to an environment in which the added microbes were not competing with field microbes. Previous field experiments using soil transfer to tree seedlings usually showed an increase in EM fungal colonization, but the presence or absence of effects on growth depended on soil provenance, field conditions, and tree species (Amaranthus and Perry, 1987; Helm and Carling, 1993; Berman and Bledsoe, 1998; Dickie *et al.*, 2007).

The main objective of this study was to evaluate the effects of adding forest soil to tree seedlings planted in an abandoned agricultural field and to follow their survival and growth over three growing seasons. The specific objective was to compare the responses of two ectomycorhizal (EM) tree species and two arbuscular mycorrhizal (AM) tree species to the different soil inoculation treatments. Since associations with EM fungi usually confer more benefits to tree seedlings than associations with AM fungi (van der Heijden and Horton, 2009; Bradford, 2014) and AM fungi should be more abundant than EM fungi in agricultural soils, a greater response from EM tree seedlings was expected. We also questioned the effect of host specificity and soil provenance: does soil inoculum collected under a mature tree of the same species have effects similar to that of inoculum collected under a different species on the receiving seedling? Since many mycorrhizal fungi are not host specific (van der Heijden and Horton, 2009), we hypothesised no effect of soil provenance.

3.3 Materials and methods

3.3.1 Study area

The experiment was conducted at the city of Montréal's tree nursery, in the suburb of L'Assomption (45°48′38″N; 73°26′26″W). The region is characterized by a humid continental climate. For the 1981-2010 period, the average annual temperature recorded at the nearest weather station (Verchères, 45°46′N; 73°22′W) is 6.6°C, with monthly means of 21°C in July and -10°C in January while average annual precipitation is 984 mm, of which almost 20% falls as snow (Environment and Climate Change Canada, 2015). The experiment

was established on two adjacent abandoned agricultural fields separated by a 5 m wide buffer of young Norway spruce (*Picea abies*). Soil is a fine to very fine sandy loam (IRDA, 2008). Fields were mown once or twice a year since the end of agricultural crop production more than 15 years ago. Mowing promoted ruderal herbaceous vegetation dominated by grass and clover species which are hosts of arbuscular mycorrhizal species.

3.3.2 Experimental design

This controlled field experiment began in May 2012 and the last growth measurements were taken at the end of the third growing season in August 2014. Four 12 × 36 m blocks were delineated in the largest abandoned field. Another block of the same size was delineated in the smallest abandoned field. Blocks were located at least 5 m away from a forested strip and more than 30 m from the road to avoid edge effects. Each block was divided into two sections: the first for AM tree species and the second for EM tree species. Two AM tree species, red ash (*Fraxinus pennsylvanica* Marshall) and red maple (*Acer rubrum* L.), and two EM tree species, yellow birch (*Betula alleghaniensis* Britton) and northern red oak (*Quercus rubra* L.), were planted. Each half block was divided into 9 plots using a random split-plot design. For the first half of each block, the treatments were: (1) soil quantities (0 ml, 300 ml or 1500 ml of loose soil); (2) soil sterilization (sterilized or not, hereinafter named live soil); (3) soil provenance (red ash or red maple forest soils) and (4) tree species (red ash or red maple) (Fig. 3.1a). For the other half of the blocks, the first two factors were the same, but the soil provenance and tree species treatments were replaced by the EM species yellow birch and red oak (Fig. 3.1b). In each plot, 3 seedlings of the same species (9 plots, 5 blocks, 4 species) were planted (total of 540 seedlings).

These four hardwood species were selected because they are native to the area and seedlings are readily available. All four species have intermediate shade tolerance (Niinemets and Valladeres, 2006). Container-produced one year-old seedlings were provided by the Berthierville nursery of the Quebec Ministry of Forests, Wildlife and Parks. This nursery does not inoculate seedlings with any microbes. Once delivered, seedlings were kept in a

dark room (4°C, 90% humidity) before planting. Seedlings were manually planted at 2 m spacing on May 14 and 15, 2012 after the herbaceous vegetation was mowed.

Following planting, a white 50 × 50 cm polyester and polypropylene felt mulch (Arbo-Pro, Texel, Saint-Elzéar-de-Beauce, Canada) was placed around each tree seedling to reduce herb competition and maintain a stable climate while allowing water to penetrate the soil. In the rows between seedlings, vegetation was mowed every month during the summer. Each tree seedling was protected from small mammal predation using a plastic tree protector (Timm Enterprises Ltd, Milton, Canada). Tree protectors were 30 cm high for red ash, red maple and red oak seedlings, and 20 cm for the smaller yellow birch seedlings. No signs of herbivory were observed.

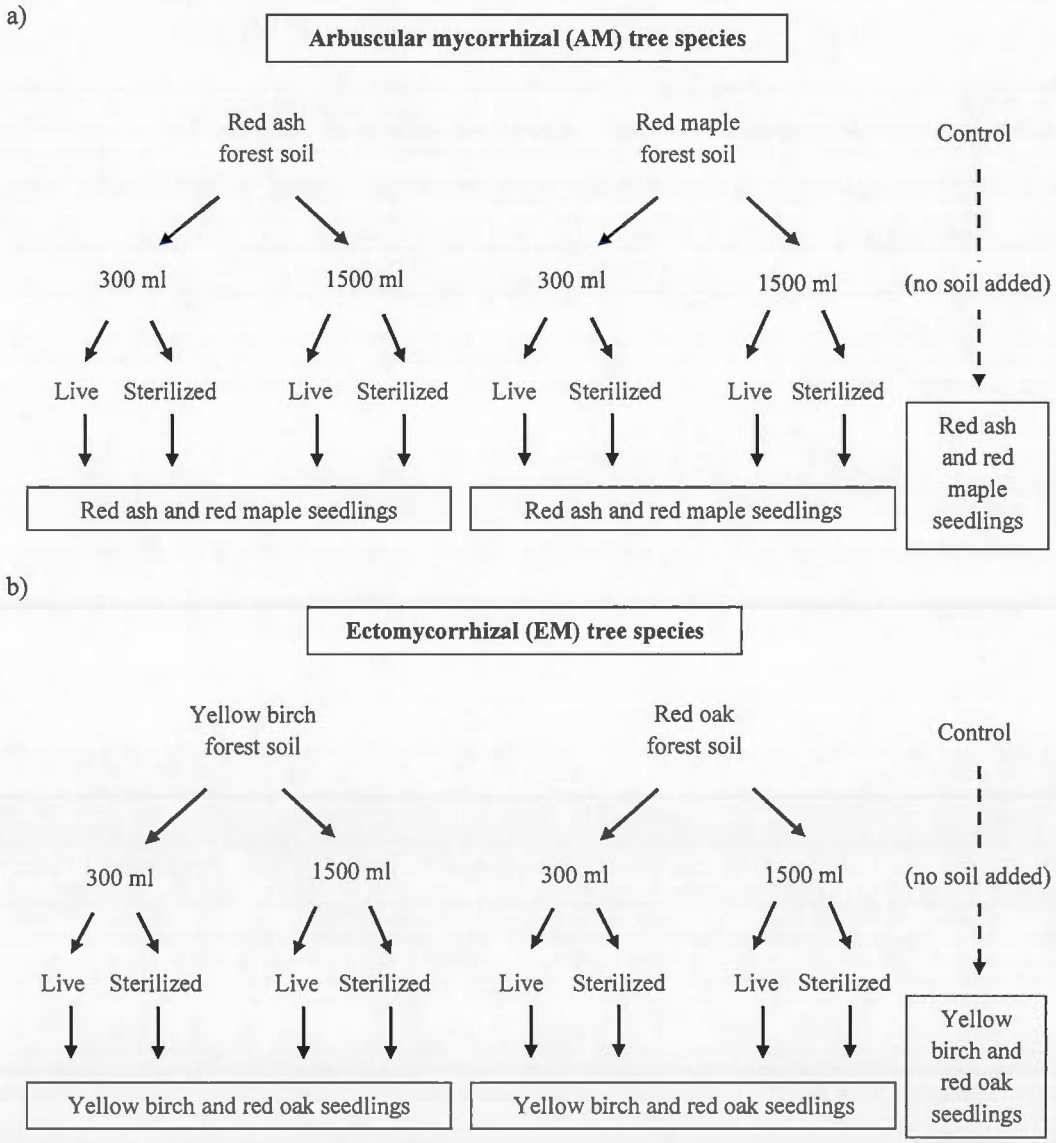


Figure 3.1 Conceptual framework of the experimental design for (a) arbuscular mycorrhizal (AM) tree species and (b) ectomycorrhizal (EM) tree species.

3.3.3 Soil collection and inoculation

Soils were collected in forest stands located within a 100 km radius of the study area between May 7 and 9, 2012. AM forest soil samples were collected in the forests in proximity to the island of Montréal, whereas EM forest soils were collected in the Lower Laurentians, starting about 60 km north of Montréal where the EM species are more abundant. More specifically, soil supporting red ash trees was collected in a woodlot outside the city of Laval, in an agricultural setting, approximately 35 km southwest of the study area (45°40′36″N; 73°43′39″W). The woodlot is composed of many broadleaf species, but the soil was taken in a section dominated by more than 70% mature red ash trees. The soil has a high activity of earthworms (A. St-Denis, pers. obs.) due to its neutral pH (calcareous glacial till). It developed into a Melanic Brunisol (Soil Classification Working Group, 1998) or Eutric Cambisol (IUSS Working Group WRB, 2015).

Soil supporting red maple trees was collected in a relatively pure red maple stand bordering a river, near the city of Boisbriand, located about 50 km southwest of the study area (45°35′52″N; 73°50′04″W). The soil developed from a fluvial deposit and transitions from Gleysols to Gray Brown Luvisol (or Albic Luvisol) (Soil Classification Working Group, 1998; IUSS Working Group WRB, 2015), depending on drainage. Soil has high P content due to previous agricultural land use on the uphill portion of the site.

Soils supporting yellow birch and red oak were collected at the *Station de biologie des Laurentides* of the *Université de Montréal*, in Saint-Hippolyte, 95 km northwest of the study area. The Precambrian Shield from which the yellow birch and red oak soils were sampled is characterized by thin glacial till soils derived from felsic (acidic) rocks (Bélanger et al., 2012) that generally develop into Orthic Humo-Ferric Podzols (Soil Classification Working Group, 1998, or Orthic Podzols, IUSS Working Group WRB, 2015). For yellow birch, soil was sampled in a sugar maple — yellow birch stand (45°58′51.3″N; 74°00′52.7″W) located on a gentle slope. For red oak, soil was collected in a sugar maple — red oak stand (45°58′17.0″N; 73°59′53.4″W) located on a hilltop. In these two stands, sugar maple was the dominant

species while yellow birch was the co-dominant species in the first one and red oak, in the other.

As microbe species and abundance could change during the growing season, another soil collection was conducted on August 16, 2012, at the same sites, but in areas undisturbed by the previous soil collection. In each forest type, soil samples were collected from under at least six mature trees (stems with DBH > 20 cm) of the target species in an area where the other tested species of the same mycorrhizal association was not present. Coarse woody debris and surface litter were removed before collecting soil (0-25 cm depth) between 0.5 and 1 m from a mature tree. To avoid contamination, collection tools were washed with a bleach solution (10% of sodium hypochlorite) and rinsed with water between each forest soil collection. All soil samples from a given forest site were combined into a single bulk sample. Bulk samples were sieved using a 1 cm mesh, but fine root segments were kept. Half of the bulk samples were immediately stored in a dark cool room (4°C, 90% of humidity) for a few days before being brought to the planting site. The other half of the bulk samples received a gamma irradiation treatment at the Nordion's Gamma Centre (Laval, Québec) to eliminate invertebrates, fungi and other microorganisms (McNamara et al. 2003). The first batch of soils was sterilised May 10 to 14, 2012, with a minimal dose of 51.1 kGy and a maximal dose of 73.9 kGy. The second batch was sterilised August 17 to 21, 2012, with a minimal dose of 54.7 kGy and a maximal dose of 80.5 kGy.

Inocula of 100 ml or 500 ml of live or sterilized soils were added in three steps for a total of 300 ml or 1500 ml of soil added. The first soil inoculum (100 or 500 ml) was placed in the planting hole just before the seedling was planted and the second was applied at the soil surface around the seedling (≈300 cm^2) immediately after planting. The third application was also at the soil surface around the seedling but three months after planting (August 16 and 21, 2012). In each block, the controls (three individuals per species) did not receive any soil inoculum.

3.3.4 Soil analyses

Subsamples of each soil type were air-dried and sieved at 2 mm before determining sand, silt and clay fractions using the hydrometer method Done (Kroestch and Wang, 2008) and soil pH in water (soil:solution ratio of 1:2.5). Organic C, total N and S were determined on finely ground samples by combustion and infrared detection (CNS 2000, LECO Corporation, MI). Phosphorus, K, Ca, Mg, Mn, Al, Fe and Na were extracted from these samples using an unbuffered Mehlich III solution (Ziadi and Sen Tren, 2007) and measured by inductively coupled plasma emission spectroscopy (Optima 7300DV, PerkinElmer, MA). Effective cation exchange capacity (CEC) was operationally defined as the sum of Ca, Mg, K, Na, Al, Fe and Mn, whereas base saturation was expressed as the sum of Ca, Mg, K and Na on CEC (Hendershot *et al.*, 2007).

3.3.5 Data collection

Survival, height and diameter at 5 cm above the ground were measured three weeks after planting (June 4, 2012), at the end of the first (September 19, 2012) and second (October 4, 2013) growing seasons, and on August 5, 2014. On September 24 2014, 15 seedlings per species (5× inoculated with 1500 ml of live soil collected in one forest, 5× inoculated with 1500 ml of live soil from the second forest and 5× from the control plots) were randomly excavated using a side-digger which can excavate 60 cm wide and 50 cm deep. Roots were stored in a freezer at −14°C until analysed.

Roots were gently washed under tap water and examined for mycorrhizal fungal colonization. For AM tree species, 25–30 root tips per seedling (approximately 1.5 cm long) were randomly selected. The ink and vinegar staining technique developed by Vierheilig *et al.* (1998) was adapted to clear and stain red ash and red maple roots. Roots were cleared by soaking them in 10% KOH at 90°C for 10 minutes for red ash roots and 3 hours for coriaceous red maple roots. After being rinsed with tap water, they were bleached with 3% H_2O_2 for 10 and 60 minutes for red ash and red maple roots, respectively. Roots were acidified in vinegar (5% acetic acid) for 10 and 60 minutes for red ash and red maple roots. They were soaked in a solution of 5% black ink (Sheaffer Skrip #94231, Sheaffer

Manufacturing Co., Fort Madison, IA) and 95% vinegar overnight at room temperature. Roots were rinsed several times with tap water acidified with a few drops of acetic acid. They were then placed in a destain solution made of 50% glycerol, 45% distilled water and 5% of HCl (1%) solution for one week. Arbuscular colonization (AC) and hyphae colonization (HC) were assessed following McGonicle et al. (1990). Arbuscules are produced by mycorrhizal fungi while hyphae may be produced by both mycorrhizal and non-mycorrhizal fungi (McGonicle et al., 1990). Each of the 25 to 30 root tips per seedling were examined under a compound microscope (200× magnification) at three locations, for a total of 75 to 90 locations examined per sample.

For EM tree species, approximately 100 1 cm root tips were randomly selected among all roots collected per excavated seedling and examined under a dissecting microscope (10-50×). EM fungal colonization for red oak and yellow birch seedlings was assessed as the proportion of root tips with mycorrhizal structures (identified by color, branching, shape, texture and presence of emanating hyphae) over the total number of root tips evaluated. A subset of 15–25 root tips/seedling was observed under a compound microscope (100–400×) to confirm the presence of a Hartig net for EM tree species.

3.3.6 Statistical analyses

Chi-square tests were used to assess seedling survival. Analyses of variance for repeated measurements (ANOVAR) and univariate analyses of variance (ANOVA) were performed for each species to evaluate the effects of soil inoculum quantity, soil sterilization, soil provenance, time and their interactions on seedling height and diameter. Analyses were performed following a split-plot design (3×2 factorial model): Block (random) × Soil inoculum quantity × Soil sterilization × Soil provenance. The data satisfied the assumptions of homoscedasticity and normality. Student's t-test and Tukey test were used as *post-hoc* tests. The statistical design was not balanced if the control plots (no soil added) were included in the analyses of variance. We thus used a 9×1 factorial model which includes 8 soil treatment combinations (for example: "300 ml of sterilized yellow birch soil") + the control. To correct for multiple comparisons, the Dunnett method was used as a *post-hoc* test

to evaluate whether treatment means were significantly different from control means. Levels of mycorrhizal fungal colonization were compared using ANOVAs and correlated to final tree height and diameter with Pearson correlations. All statistical analyses were performed using JMP 10.0. Statistical significance was determined at $p = 0.05$.

3.4 Results

3.4.1 Soil characteristics

Basic physical and chemical characteristics of forest and agricultural field soils are presented in Table 3.1. On the one hand, very high and high levels of extractable (Melhich III) P were measured for the agricultural soil (68 mg kg^{-1}) and for red maple soil (40 mg kg^{-1}), respectively, compared to the other forest soil types (ranging from 6 to 23 mg kg^{-1}). On the other hand, the agricultural field soil had the lowest organic C (1.44%) and total N (0.13%) levels and some of the lowest exchangeable Ca (5.12 $cmol_{(+)}$ kg^{-1}), CEC (31.4 $cmol_{(+)}$ kg^{-1}) and base saturation (19.8%) values in comparison to forest soils (2.93-13.0% for organic C; 0.32-0.64% for total N; 1.18-29.9 $cmol_{(+)}$ kg^{-1} for exchangeable Ca; 10.5-44.4 $cmol_{(+)}$ kg^{-1} for CEC and 3.91-73.0% for base saturation). The molar N (total): P (Mehlich) ratio of the agricultural field soil (42.2) was much lower than all other forest soils (174-2257) (results not shown). The AM soils showed higher exchangeable Ca, base saturation and pH than the EM soils. Soils collected under mature red ash trees had the highest exchangeable Ca (28-30 $cmol_{(+)}$ kg^{-1}), base saturation (71-73%) and pH (7.25). The red ash and red maple soils had relatively high silt and clay content, whereas the more acidic yellow birch and red oak soils had coarser texture (i.e. sandy loam).

Table 3.1 Soil characteristics of the experimental abandoned agricultural field and four forest stands (soil taken under mature trees of red ash, red maple, yellow birch and red oak)

Soil types	Sterile ?	Sand %	Silt %	Clay %	Organic C %	Total N %	Total S %	P Mehlich mg/kg	Exch. Ca cmol (+)/kg	Exch. Al cmol (+)/kg	C.E.C cmol (+)/kg	Base saturation (%)	pH
Agricultural field	-	62	27.5	10.5	1.44	0.13	0.03	68.2	5.12	23.6	31.4	19.8	6.2
Red ash soil	No	36.2	38.8	25	7.08	0.52	0.07	8.39	29.9	12.1	45.8	71.1	7.2
	Yes	40	28.8	31.2	8.39	0.64	0.10	22.8	28.5	10.5	42.70	73.0	7.3
Red maple soil	No	5	56.2	38.8	2.93	0.32	0.07	40.5	7.92	23.3	36.7	31.2	4.9
	Yes	13.8	41.2	45	3.02	0.33	0.08	40.0	7.80	23.9	37.1	30.2	5.1
Yellow birch soil	No	66.2	23.8	10	12.8	0.61	0.13	5.99	2.01	40.9	44.7	6.13	4.4
	Yes	65	22.5	12.5	11.8	0.55	0.11	10.4	2.03	44.4	48.7	5.61	4.4
Red oak soil	No	60	28.8	11.2	13.0	0.63	0.13	7.00	1.18	43.7	46.6	3.91	4.5
	Yes	58.8	30	11.2	11.7	0.61	0.11	11.6	2.03	44.0	47.9	5.88	4.7

Exch. is exchangeable; C.E.C. is effective cation exchange capacity

3.4.2 Survival

Seedling survival was high, with no mortality for red ash seedlings, one tree lost for red maple and five for red oak seedlings. Mortality was too low for chi-square tests, except for the EM species yellow birch (22 dead seedlings). However, neither soil inoculum quantity ($\chi^2 = 0.374$; $p = 0.5410$), sterilization ($\chi^2 = 1.016$; $p = 0.3135$) nor soil provenance ($\chi^2 = 1.330$; $p = 0.2488$) affected survival.

3.4.3 Effects of soil treatments on AM tree species growth

AM tree species did not show consistent or persistent responses to the addition of forest soil. None of the factors tested affected red ash height and diameter (Tables 3.2–3.3, Fig. 3.2). However, after the first growing season (in the fall of 2012), the diameter of red ash seedlings receiving 1500 ml of live red maple soil ($p = 0.01$) and 300 or 1500 ml of sterilized red ash soil ($p = 0.04$ and $p = 0.01$, respectively) was larger than the diameter of seedlings that did not receive forest soil (Fig. 3.2b). These effects did not persist with time ($F = 0.74$, $p = 0.74$; Table 3.2).

The growth of red maple seedlings inoculated with forest soil was similar to the growth of seedlings in the control (Fig. 3.3). However, a significant "soil inoculum quantity" × "soil sterilization" × "soil provenance" interaction ($F = 10.99$, $p = 0.001$) was detected for red maple height at the end of the first growing season (Table 3.3). Red maple seedlings inoculated with 1500 ml of live red ash soil were taller than seedlings receiving 300 ml, and taller than those inoculated with 1500 ml of live red maple soil. Conversely, red maple seedlings inoculated with soil collected under conspecific trees were taller than those inoculated with red ash soil, but only when 300 ml of live soil was added. These contrasting results do not provide strong evidence for positive effects of forest soil inoculation on red maple seedlings.

Table 3.2 ANOVAR results for the height and diameter of red ash, red maple, yellow birch and red oak seedlings as influenced by soil quantity, soil sterilization, soil provenance, in interaction with time (three growing seasons included)

		Height		Diameter	
	d df	*F*	*P*	*F*	*P*
Red ash					
Quantity × Time	79	0.2970	0.7438	0.1380	0.8713
Sterilization × Time	79	1.5395	0.2209	0.3885	0.6794
Provenance × Time	79	0.5507	0.5788	0.6260	0.5374
*Treatments × Time	178	0.8449	0.6334	0.7414	0.7488
Red maple					
Quantity × Time	78	0.9192	0.4031	0.2267	0.7977
Sterilization × Time	78	1.6824	0.1926	4.1762	*0.0189*
Provenance × Time	78	0.0254	0.9749	0.6182	0.5415
*Treatments × Time	176	0.8821	0.5906	1.0617	0.3952
Yellow birch					
Quantity × Time	61	4.7287	*0.0123*	2.0779	0.1340
Sterilization × Time	61	1.4381	0.2453	0.8062	0.4513
Provenance × Time	61	0.5528	0.5728	1.3599	0.2644
*Treatments × Time	132	1.8205	*0.0345*	1.3528	0.1754
Red oak					
Quantity × Time	74	9.7903	*0.0002*	5.7884	0.0046
Sterilization × Time	74	2.1813	0.1201	2.4714	0.0914
Provenance × Time	74	0.5650	0.5708	0.3299	0.7200
*Treatments × Time	168	2.3605	*0.0034*	1.8556	0.0279

*The fixed effect "Treatments" is the combination of the three levels of soil treatments (i.e. soil quantity, sterilization and provenance). It includes control seedlings (no soil added). *F* was estimated with Wilks' Lambda.

Table 3.3 ANOVA results for the height and diameter of red ash, red maple, yellow birch and red oak seedlings as influenced by soil quantity, soil sterilization, soil provenance, and their interactions after the first season of growth (Fall 2012)

	Height			Diameter		
	d df	*F*	*P*	d df	*F*	*P*
Red ash						
Quantity (Q)	4	0.0478	0.8376	4	0.0813	0.7897
Sterilization (S)	4	3.9775	0.1169	4	0.1727	0.6990
Provenance (P)	4	0.5230	0.5096	4	0.0456	0.8413
Q × S	4	8.1203	*0.0464*	4	1.1627	0.3416
Q × P	4	0.5037	0.5170	4	0.0002	0.9902
S × P	4	0.0137	0.9124	4	1.5584	0.2800
Q × S × P	84	0.0246	0.8757	84	1.0218	0.3150
Red maple						
Quantity (Q)	4.098	0.1917	0.6836	4.049	0.0102	0.9245
Sterilization (S)	4.006	0.0249	0.8822	4.032	0.0000	0.9968
Provenance (P)	3.978	5.6159	0.0772	4.051	4.8818	0.0908
Q × S	3.969	0.0125	0.9164	4.032	0.5406	0.5027
Q × P	4.103	4.7126	0.0940	4.035	0.0105	0.9234
S × P	4.072	1.5456	0.2806	3.952	0.2183	0.6649
Q × S × P	83.69	10.9947	*0.0014*	83.36	0.2855	0.5945
Yellow birch						
Quantity (Q)	4.091	0.8417	0.4097	4.054	0.2624	0.6351
Sterilization (S)	4.048	32.4920	*0.0045*	3.775	18.2019	*0.0147*
Provenance (P)	4.118	1.5048	0.2854	3.991	0.0004	0.9842
Q × S	3.746	13.5497	*0.0238*	3.981	5.8119	0.0738
Q × P	4.195	0.0177	0.9002	3.321	90.2128	*0.0016*
S × P	3.812	0.0047	0.9488	3.88	1.8863	0.2436
Q × S × P	81.21	3.0652	0.0838	80.42	0.0048	0.9448
Red oak						
Quantity (Q)	4	27.7657	*0.0062*	4	0.0556	0.8252
Sterilization (S)	4	11.3113	*0.0282*	4	1.7069	0.2614
Provenance (P)	4	27.2911	*0.0064*	4	0.8336	0.4129
Q × S	4	6.3561	0.0653	4	1.1078	0.3519
Q × P	4	0.9235	0.3910	4	0.0005	0.9835
S × P	4	1.7141	0.2606	4	0.5369	0.5043
Q × S × P	84	0.0828	0.77472	84	0.0129	0.9097

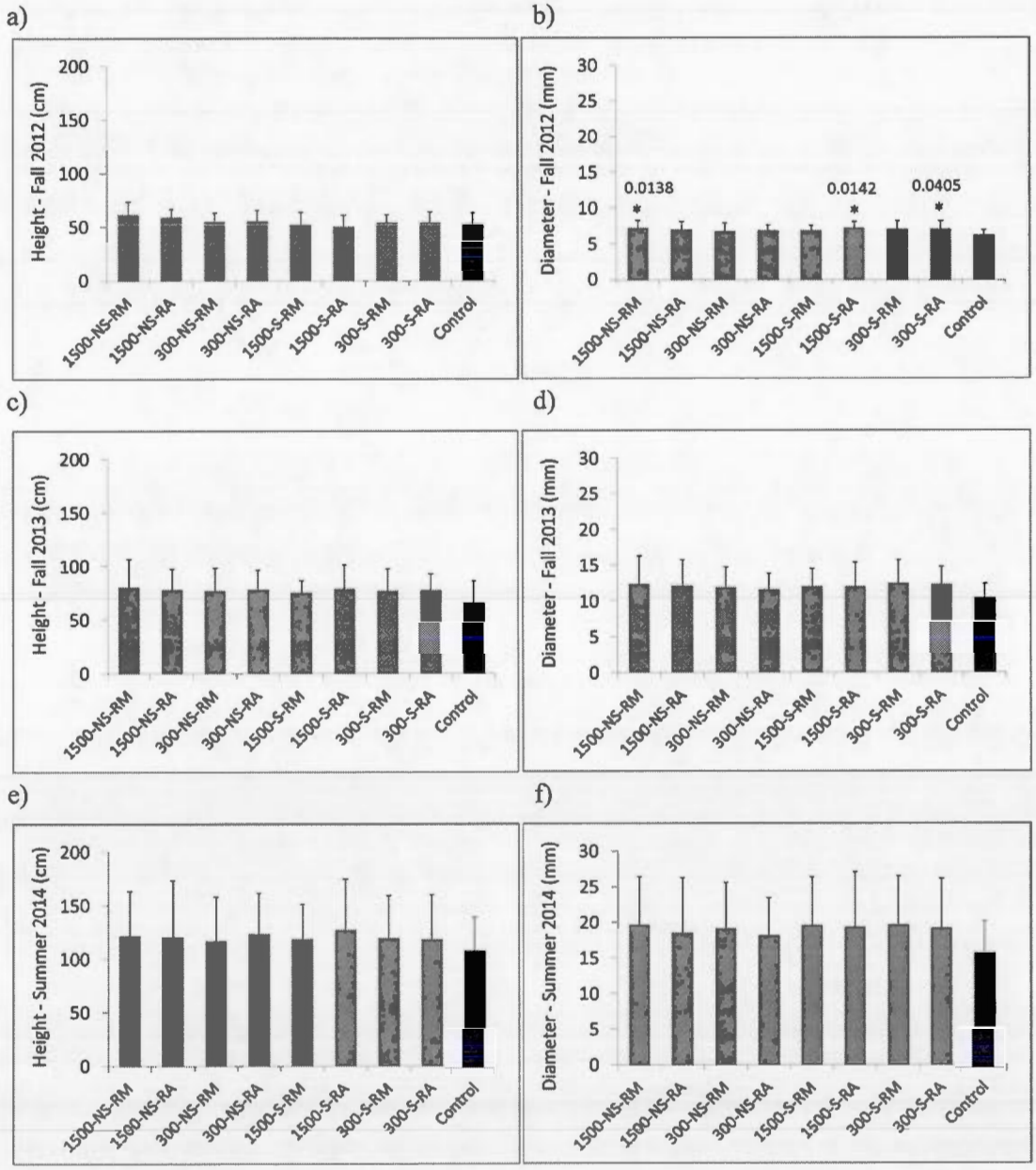


Figure 3.2 Height and diameter (mean ± sd) of red ash seedlings in the eight combined soil treatments compared to the control in a) and b) fall of 2012; c) and d) fall of 2013; and e) and f) summer of 2014.

Combined soil treatments: Inoculation with 1500 ml (**1500**) or 300 ml (**300**) of forest soil, with live soil (**NS** = non sterilized) or sterilized soil (**S**); and with soil collected under mature red maple trees (**RM**) or mature red ash trees (**RA**). An asterisk (preceded by the *p*-value) indicates that the mean differs from the mean of the control (Dunnett's test).

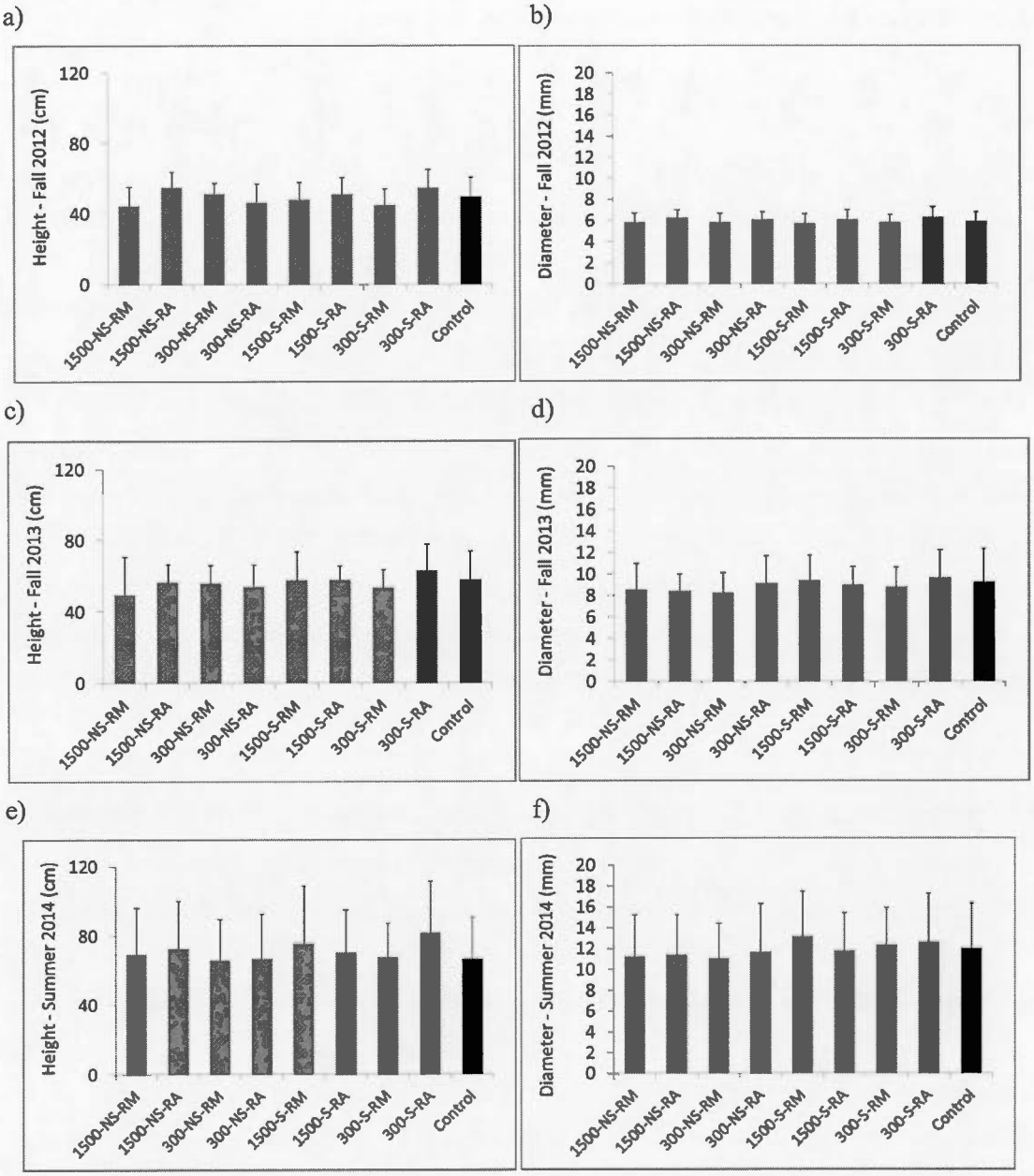


Figure 3.3 Height and diameter (mean ± sd) of red maple seedlings in the eight combined soil treatments compared to the control in a) and b) fall of 2012; c) and d) fall of 2013; and e) and f) summer of 2014.

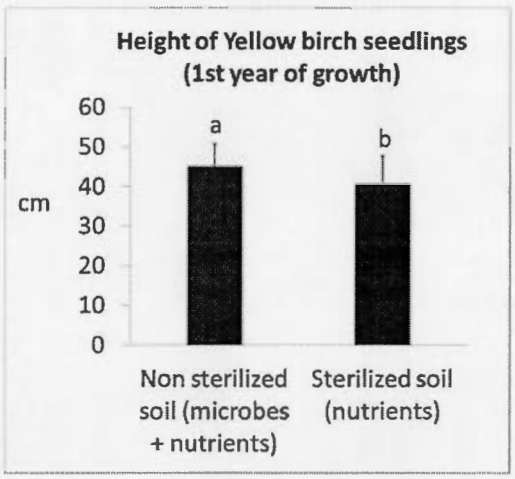
3.4.4 Effects of soil treatments on EM tree species growth

The EM birch seedlings inoculated with live soil were taller and had a larger diameter during the first year (F = 32.49, p = 0.005 and F = 18.20, p =0.01, respectively) than those inoculated with sterilized soil for all soil quantities and provenances combined (Fig. 3.4; Table 3.3). Furthermore, yellow birch seedlings inoculated with sterilized soil (1500 ml of yellow birch soil, 300 or 1500 ml of red oak soil) were smaller than control seedlings at the end of the first growing season (Fig. 3.5a). The effect on height was greater when 1500 ml of soil was added vs 300 ml (F = 13.55, p = 0.02; Table 3.3). In contrast to height, yellow birch seedlings inoculated with yellow birch soil (sterilized or not) had a larger diameter when 300 ml of soil was added instead of 1500 ml (F = 90.21, p = 0.002; Table 3.3). This was only observed after one growing season. By the end of the third season, results had reversed such that diameter growth of birch seedlings inoculated with 1500 ml of live soil was greater than with 300 ml (F = 14.49; p = 0.02). Moreover, after the third year of growth, seedlings receiving 1500 ml of live red oak soil had a larger diameter than controls (p = 0.005; Fig. 3.5f). These effects coupled with the first year effects suggest some benefits of adding live red oak soil to yellow birch seedlings when planting it in an abandoned agricultural field.

Positive and negative feedbacks were observed on the growth of red oak seedlings. Oak seedlings inoculated with live (1500 ml) or sterilized red oak soil (300 or 1500 ml) were smaller than control seedlings after the first and second growing seasons (Fig. 3.6a,c). As with the other EM species, red oak seedlings were taller when inoculated with live soil vs sterilized soil after the first year (F = 11.31, p = 0.03; Fig. 3.7a; Table 3.3). Also, they were tallest when a small quantity of soil was added (F = 27.77, p = 0.006; Fig. 3.7b). First year red oak seedlings inoculated with red oak soil were smaller than those inoculated with yellow birch soil (F =27.29, p = 0.006; Fig. 3.7c). At the end of the third summer, red oak seedling diameters were larger when inoculated with 1500 ml of soil instead of 300 ml (F = 11.21, p = 0.03). In contrast to height growth, diameter growth did not differ between the soil treatments and the control (Fig. 3.6). In summary, for red oak seedlings, we observed: (1) a positive effect of adding live compared to sterilized soil; (2) a positive effect of adding yellow birch soil compared to red oak soil (although there were no significant benefits of adding forest soil

compared to the control) (Fig. 3.6); and finally (3) a negative feedback of live red oak soil on red oak seedling height.

a)



b)

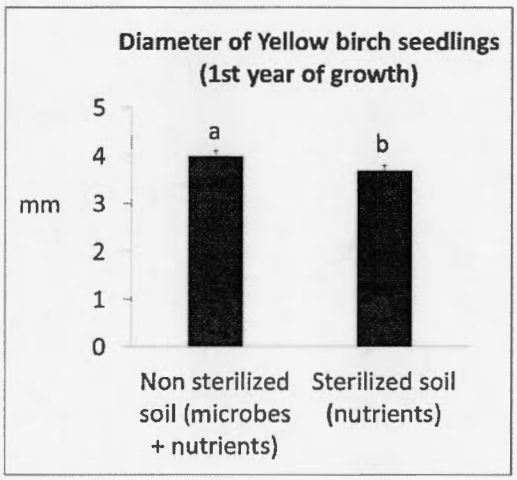


Figure 3.4 (a) Height and (b) diameter (mean ± sd) of yellow birch seedlings after one season of growth (fall 2012) according to sterilization: non sterilized (live) soil *vs* sterilized soil.

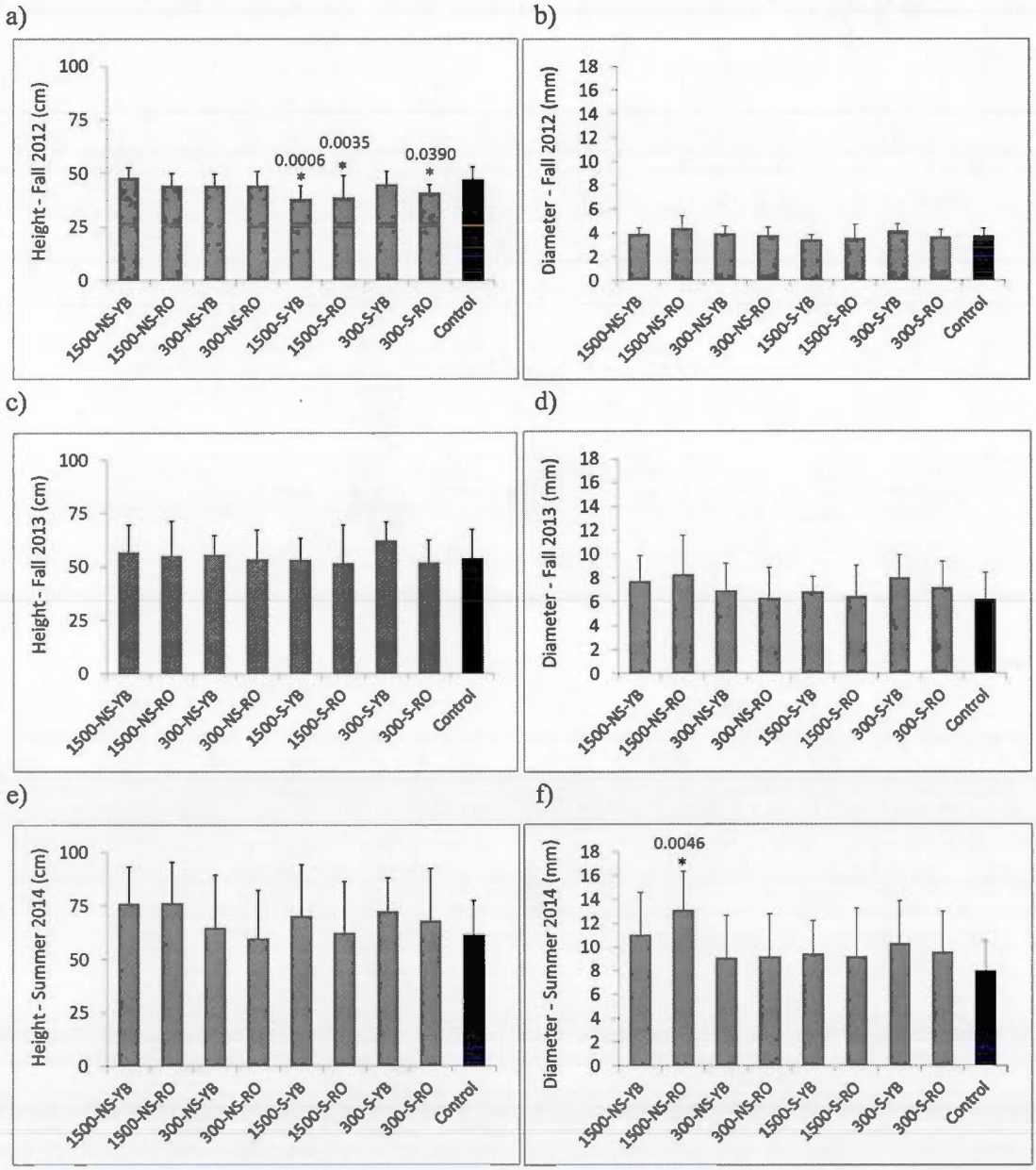


Figure 3.5 Height and diameter (mean ± sd) of yellow birch seedlings in the eight combined soil treatments compared to the control in a) and b) fall of 2012; c) and d) fall of 2013; and e) and f) summer of 2014.

Combined soil treatments: Inoculation with 1500 ml (**1500**) or 300 ml (**300**) of forest soil, with live soil (**NS** = non sterilized) or sterilized soil (**S**); and with soil collected under mature yellow birch trees (**YB**) or mature red oak trees (**RO**). An asterisk (preceded by the *p*-value) indicates that the mean differs from the mean of the control (Dunnett's test).

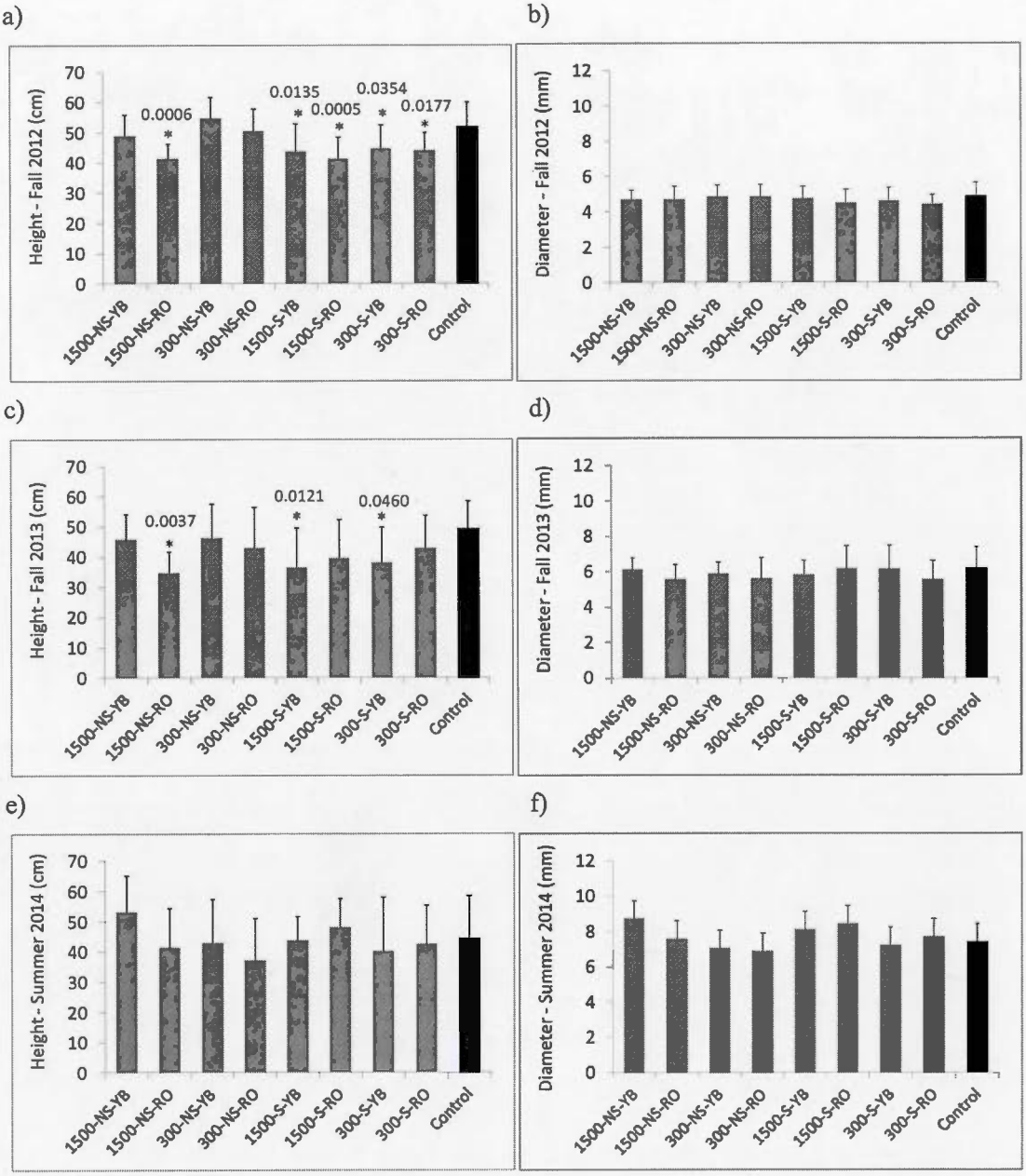
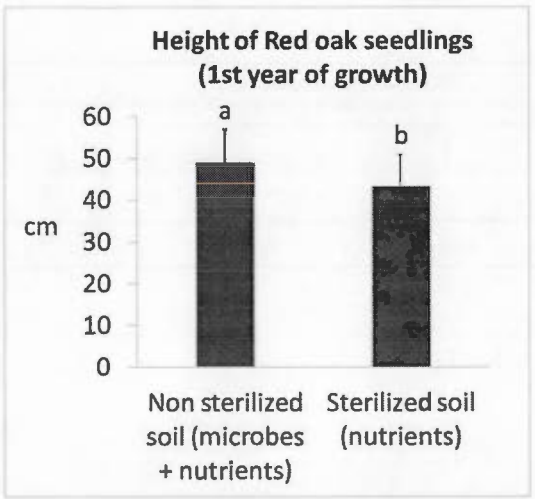
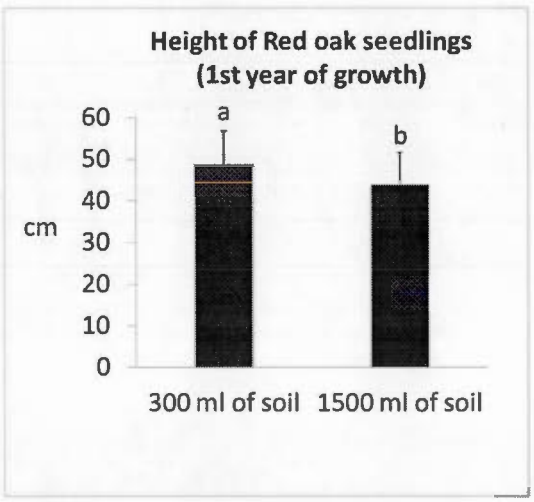


Figure 3.6 Height and diameter (mean ± sd) of red oak seedlings in the eight combined soil treatments compared to the control in a) and b) fall of 2012; c) and d) fall of 2013; and e) and f) summer of 2014. An asterisk (preceded by the *p*-value) indicates that the mean differs from the mean of the control (Dunnett's test).

a)



b)



c)

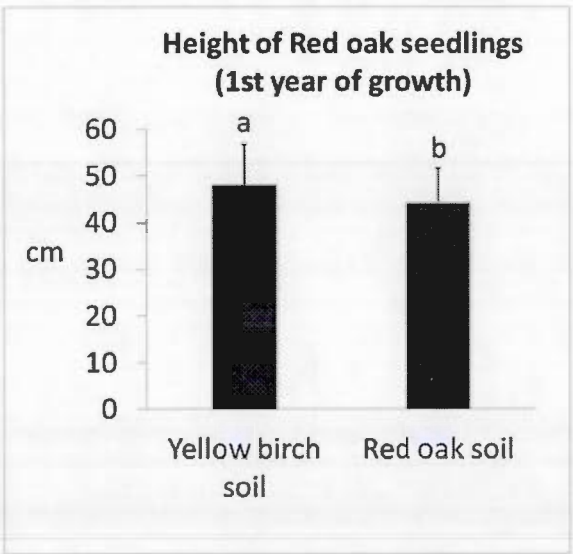


Figure 3.7 Height (mean ± sd) of red oak seedlings after one growing season (fall 2012) according to a) sterilization; b) soil quantity; and c) soil provenance.

3.4.5 Mycorrhizal fungal colonization

We observed >75% hyphae colonization (HC) for ash and maple seedlings. Forest soil inoculation did not increase arbuscular colonization (AC) of red ash (34 to 51%; $F = 1.09$, $p = 0.38$) and red maple seedlings (68 to 70%; $F = 1.89$, $p = 0.95$) nor the EM fungal colonization of yellow birch (40 to 60%; $F = 0.94$, $p = 0.43$) or red oak seedlings (30 to 43%; $F = 2.02$, $p = 0.19$). Hypha of EM fungi observed on EM tree roots were less than 5 cm long. Mycorrhizal fungal colonization was not correlated to tree height ($p > 0.19$) and diameter ($p > 0.22$).

3.5 Discussion

3.5.1 AM vs. EM tree species response

We hypothesized a greater response from EM tree seedlings than AM tree seedlings and no effect of soil provenance because many mycorrhizal fungi are not host specific (van der Heijden and Horton, 2009). As expected, forest soil inoculum had more effects on EM than on AM tree species. On the one hand, only few temporary, weak or divergent effects were observed for the growth of both AM tree species. On the other hand, yellow birch and red oak seedlings responded positively to the inoculation of live soil compared to sterilized soil in the first growing season, suggesting a possible microbial feedback. Moreover, birch seedlings receiving 1500 ml of live soil collected under the trees of the other EM species (red oak) had a greater diameter than control seedlings after three growing seasons. This effect could be driven by microbes since birch seedlings inoculated with nutrient poor sterilized red oak soil were smaller than control seedlings after one growing season.

The increase in yellow birch diameter was noted despite similar rates of mycorrhizal infection measured in the third growing season. In fact, adding forest soil did not influence mycorrhizal infection of any AM or EM tree species. The number of seedlings excavated might have been too few (5 per species per treatment) to detect an effect, especially since, in some cases, mycorrhizal fungal colonization varied considerably within a treatment. Furthermore, tree seedlings produced in nurseries can be naturally colonized by spore inoculation, but tree seedlings growing in forests may have more and different mycorrhizal

fungal species (Gagnon *et al.*, 1991; Southworth *et al.*, 2009). As we conducted our study as a restoration project to test whether forest soil inoculation would affect tree survival and growth, we did not identify the mycorrhizal fungal species. Also, we did not measure the mycorrhizal fungal colonization within the first year. The differences in mycorrhizal infection between soil treatments might be greater after one season of growth and then fade with time (Dickie *et al.*, 2007). This could explain the first year effects identified on EM tree species which benefited from live forest soil inoculation compared to the addition of sterilized soil.

The greater responses of EM tree species than AM tree species are consistent with the literature. First, the density of AM fungi increases with time since abandonment until a shift occurs in the plant community from herbaceous vegetation to woody ectomycorrhizal hosts (Johnson *et al.*, 1991). Thus, AM fungi are suspected to be more abundant than EM fungi in old fields. Second, EM tree species usually benefit more from mycorrhizal fungal associations than AM tree species, because exchange between mycorrhizal fungi and trees are greater for EM species than AM species (van der Heijden and Horton, 2009, Bradford, 2014) Third, soil nutrient availability in the field may have been more beneficial to EM fungi than AM fungi. Mycorrhizal fungal colonization increases and provides more benefits for seedlings in nutrient-limited environments, particularly in soils with low P availability in the case of AM species and in soils with low N availability in the case of EM species (Jonsson *et al.*, 2001; Wiseman and Wells, 2005; Reynolds *et al.*, 2005; Smith and Read, 2008). Although the low organic C and total N levels of the agricultural soil was expected, we did not anticipate such a high level of extractable P (i.e. 68 mg P kg^{-1}, whereas Sawyer *et al.* (2002) proposed that relative yields of most crops are expected to be optimal between 26 and 35 mg P kg^{-1}, Mehlich III). As a whole, the low molar N:P ratio of the agricultural soil suggests a low availability in N relative to P. This may explain the few positive effects of forest soil inoculation, principally for AM tree species, as well as the lack of positive correlations between mycorrhizal fungal infection and tree growth. Furthermore, when a productive soil has low C levels, plant growth can be slightly reduced because the C demand

of mycorrhizal fungi and mycorrhizal associations can shift from a mutualistic to a parasitic relationship (e.g. Johnson *et al.*, 1997).

The study site was covered by AM grass and clover species. Since AM fungi are not host specific (Klironomos, 2000; van der Heijden and Horton, 2009), AM tree seedlings may have been colonized by AM fungi present in the agricultural field abandoned for more than 15 years. In addition, the generalist red ash and red maple species are well adapted to these environments as they are among the first to invade abandoned fields in our area (D'Orangeville *et al.*, 2008). Open fields may contain ectomycorrhizal propagules, but ectomycorrhizas (EM) are more abundant and diverse in forests (Berman and Bledsoe, 1998). Our results suggest that restoration of EM tree species in abandoned agricultural fields may benefit more from forest soil additions than AM tree species. Similarly, the growth of an AM tree species (western red cedar seedlings) was improved by AM myccorhizal inoculum when planted in ectomycorrhizal-dominated hemlock-amabilis fir clearcuts (Guichon, 2015).

3.5.2 The effects of soil provenance

Contrary to our initial hypothesis, soil provenance somewhat influenced the results such as a positive effect of red oak soil on yellow birch seedlings. Conversely, one EM tree species responded negatively to the addition of forest soil collected under conspecific trees. Red oak seedlings inoculated with red oak soil were smaller than those inoculated with yellow birch soil and control seedlings. This negative feedback on red oak seedling height was also observed when sterilized red oak soil was added, probably due to its low P content, 8 times lower than that of the agricultural field soil, as well as lower exchangeable Ca, base saturation and pH (<5). The negative effect observed in the first year following the inoculation of live red oak soil persisted through the second growing season. In addition to its lower nutrient availability, it may be due to its pathogens because seedlings inoculated with 1500 ml of live red oak soil were smaller than those in the control, whereas those that had received 1500 ml of sterilized oak soil were no longer different from the control in the second year of growth.

This negative conspecific effect provides some support for the Janzen-Connell hypothesis (JCH). The JCH stipulates that mature individuals of a same tree species increase the abundance in their vicinity of common enemies potentially inducing a negative feedback on seedling survival and growth (Janzen 1970; Connell 1971). These enemies can be aboveground organisms (e.g. mammals, herbivores, insects, foliar pathogens), but the effect is considered to be mainly driven by soil microbes (Bever *et al.*, 2010; Mangan *et al.*, 2010). Since only one of the four temperate species studied responded negatively to live soil inoculation collected under conspecific trees, our results suggest that tree species have different sensitivity to negative–density dependent regulation induced by microorganisms. Due to harsher environmental conditions or the smaller impact of biotic interactions (see review by Schemske *et al.*, 2009), the strength of the negative density-dependent effect is suggested to fade with increasing latitude (Janzen, 1970; Connell, 1971; Hille Ris Lambers *et al.*, 2002). Yet, Packer and Clay (2000) concluded that similar ecological mechanisms operate in temperate and tropical ecosystems after observing a strong distance–dependent effect of soil pathogens *Pythium* spp. on the survival of *Prunus serotina* seedlings grown in pots filled with soils collected under conspecific trees.

Conversely, positive interactions due to ectomycorrhizal fungi were observed on seedlings grown in soils collected under conspecific trees (Dickie *et al.*, 2007; O'Brien *et al.*, 2011). In our experiment, the absence of significant effects for some tree species may be related to a balance between the negative effects due to soil pathogens and the positive effects due to mutualist species such as mycorrhizal fungi and N-fixing bacteria.

3.5.3 The effects of soil inoculum quantity, nutrient availability, and time

Generally, stronger (positive or negative) effects were observed with 1500 ml of forest soil inoculum instead of 300 ml. The impact of soil inoculum quantity on tree growth could be explained by the level of nutrient availability found in the forest soils compared to the agricultural field soil. For example, the negative effects observed on EM tree growth when sterilized soil was added could be due to the lower nutrient availability in EM forest soils, i.e. when more forest soil was added, seedling roots likely had lower access to nutrients than the

field soil due to a ''dilution'' effect. In contrast, red maple seedlings inoculated with 1500 ml of live red ash forest soil, which has higher pH, Ca levels and base saturation than the agricultural soil, were taller after one season of growth than those that received only 300 ml.

A slight increase in red ash diameter following the addition of 1500 ml of live red maple soil or the addition of sterilized red ash soil was also observed. In these cases, growth responses may have been influenced by P levels in the added soils. Red maple soil (sterilized or not) has high levels of extractable P (i.e. 40 mg kg^{-1}) and sterilized red ash soil (23 mg kg^{-1}, near optimal range) contains more extractable P than the live red ash soil (8 mg kg^{-1}, within very low range) (see Sawyer et al. (2002) for reference P levels (Mehlich III) for most crops). The difference in P levels between live and sterilized red ash soil could be related to gamma irradiation which is highly effective for sterilization, but may have some effects on soil chemical properties such as an increase in exchangeable soil P levels (McNamara *et al.* 2003). The impact of gamma irradiation on forest soil was higher for red ash soil probably due to the high activity of earthworms and microbes in this Melanic Brunisol. On the one hand, the dead earthworms and microbes following soil sterilization have decomposed and thus likely increased soil P availability by creating a short-term pulse. On the other hand, microbial recolonization of the soil will be required to promote mobilization of bound P reserves.

The effect of soil inoculum quantity varied over time for EM tree growth. After one growing season, negative effects on birch and oak seedlings were observed when 1500 ml of live soil was added, but after three growing seasons, those seedlings had a larger diameter. Dickie *et al.* (2007) also observed that oak seedling responses varied with the quantity of forest soil added as well as time. They showed that first year seedlings receiving 2 litres of forest soil (instead of 200 ml or 0 ml) had a higher EM infection rate but a lower shoot biomass, while third year seedlings had similar EM infection but a higher leaf mass. The effect on initial aerial growth may be due to resource allocation to roots and mycorrhizas.

Most effects observed after the first growing season did not persist. Generally, by the third year, tree growth was similar in all treatments. In contrast to pot studies, inoculated microbes could have been outcompeted by field microbes. The lack of persistent effects may also be due to tree roots extending with time beyond the area where forest soil was added. Mechanical site preparation effects on EM tree seedling growth have been found to disappear when roots grew beyond the modified patches in undisturbed soils covered by AM herbaceous plants (Simard *et al.*, 2003). In our study, third year growth effects were only observed for yellow birch seedlings, the species with the smallest root system (A. St-Denis, pers. obs.), previously inoculated with 1500 ml of live red oak soil.

3.6 Conclusion

Adding live forest soil to tree seedlings planted in abandoned agricultural fields did not affect tree survival. Some positive effects of forest soil inoculation were observed on EM tree growth whereas few effects were observed on AM tree growth. The more important effect was an increase in diameter after three growing seasons for yellow birch seedlings inoculated with 1500 ml of red oak soil. Only one species responded negatively to the addition of forest soil collected under conspecific trees, suggesting that red oak growth is sensitive to conspecific accumulation of soil enemies in agreement with the Janzen-Connell hypothesis. Future research should evaluate the reasons behind the conspecific negative effect on red oak growth by isolating and identifying soil pathogens.

We suggest that the lack of persistent effects of forest soil inoculation on tree seedlings was due to (1) the possible presence of mycorrhizal fungal spores in agricultural soil and in the seedling potting-mix; (2) the conflicting positive and negative effects of adding soil containing both possible beneficial and antagonistic microorganisms; (3) the low organic C and high P levels of the agricultural soil; and (4) the nutrient dilution effect of adding a soil inoculum with lower nutrients to the bulk soil with higher nutrient availability. Because the effects of facilitation tend to increase as site fertility decreases, notably in soils with low P availability in the case of AM species (Smith and Read 2008; Brooker *et al.*, 2008), a similar experiment may show more benefits if it was repeated on less P-rich soils (or less nutrient-

rich in general) or on soils with low water retention capacity (ex. sand or loamy sand soils with a very low clay fraction). Nevertheless, this study supports the idea that planting EM tree species in abandoned agricultural field soils could benefit more from the inoculation of forest soil microbes than AM tree species.

3.7 Acknowledgements

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CONCLUSION

4.1 Une vue d'ensemble de la thèse

La restauration de terres agricoles abandonnées et de friches herbacées est appelée à augmenter un peu partout dans le monde afin de ralentir et même renverser la perte de surface forestière que la planète subit depuis le début de l'expansion humaine. Elle peut aussi être utilisée pour créer des corridors forestiers, des habitats pour des espèces rares, pour contrer l'invasion par les espèces exotiques ou pour promouvoir des biens et services écosystémiques (Society for Ecological Restoration International Science & Policy Working Group, 2004; Funk *et al.*, 2008). La restauration écologique joue aussi un rôle essentiel dans le maintien de la biodiversité et des fonctions écosystémiques (Funk *et al.*, 2008). Ainsi, la restauration doit viser à établir le plus grand nombre d'espèces ayant des caractéristiques écologiques diversifiées afin d'assurer une plus grande résilience possible. L'efficacité peut augmenter en introduisant seulement des espèces qui performent bien, mais cela pourrait ne pas maintenir la biodiversité (Pywell *et al.*, 2003). Cette thèse a permis de tester certaines techniques traditionnelles et novatrices de restauration forestière de terres agricoles abandonnées sur plusieurs espèces d'arbres de la forêt tempérée du nord-est américain.

Nos résultats de l'expérience de l'ensemencement supportent l'hypothèse que la taille des semences est le principal facteur influençant l'établissement (germination + survie) en champ (Chapitre 1). De plus, nous avons montré que la germination, la survie et la croissance en hauteur des trois espèces d'arbres ayant germé n'avaient pas été influencées par la prédation par les oiseaux ou les petits mammifères ni par la végétation herbacée. Cependant la végétation herbacée a eu des effets négatifs sur la croissance en diamètre du chêne rouge et sa biomasse aérienne. La prédation des semences, mais surtout celle des semis, sont

normalement courantes dans les friches herbacées (Ostfeld *et al.*, 1997 ; Manson *et al.*, 2001). Toutefois, des dommages faits par les petits rongeurs ont été vus sur les jeunes arbres plantés à proximité des blocs expérimentaux de l'expérience d'ensemencement (Chapitre 2). L'abondance de nourriture sur le site (plus de 15 000 arbres et arbustes ont y été plantés pendant l'expérience « ensemencement ») ainsi que la faible taille des semis issus de l'ensemencement seraient à l'origine de l'absence de prédation.

Le succès de l'ensemencement du chêne rouge et du chêne à gros fruits (Chapitre 1), deux espèces semi-tolérantes à l'ombre, barochores et ayant de larges semences, est étonnant dans la mesure où les espèces qui colonisent les terres agricoles abandonnées sont habituellement des espèces ayant de petites semences et des espèces anémochores (Hill *et al.*, 1995; D'Orangeville *et al.*, 2008). Cela laisse supposer que les espèces ayant des larges semences comme les chênes seraient absentes des friches herbacées non pas en raison d'un faible taux de germination ou de survie, mais bien en raison d'un manque de géniteurs et d'une faible capacité de dispersion, au contraire des espèces anémochores (Zimmerman *et al.*, 2000; McEuen et Curran, 2004). En outre, nos résultats appuient l'hypothèse que les espèces ayant de larges semences et étant modérément à hautement tolérantes à l'ombre germent et survivent bien lorsqu'elles sont ensemencées dans les friches herbacées, comme cela avait été démontré en milieu tropical (Hooper *et al.*, 2002; Doust *et al.*, 2006) et tempéré (De Steven, 1991a; Laliberté *et al.*, 2008a).

La croissance des espèces non-pionnières, modérément à hautement tolérantes à l'ombre, serait toutefois davantage affectée par la compétition herbacée que les espèces pionnières, puisque ces dernières ont un taux de croissance élevée qui leur permet de dépasser rapidement le couvert herbacé (Doust *et al.*, 2008). Dans notre étude utilisant des jeunes arbres plantés en champ (Chapitre 2), nous avons effectivement constaté des taux de croissance plus élevés chez la majorité des espèces pionnières. Cependant, ce serait la balance à long terme entre les taux de survie et les taux de croissance dans la végétation herbacée qui déterminerait si les espèces arborescentes sont inhibées par les espèces herbacées ou si elles y sont tolérantes (De Steven, 1991b). Ainsi, des espèces ayant une

bonne survie peuvent être considérées tolérantes malgré des taux de croissance ralentis par la végétation, car elles finiront par dépasser le couvert herbacé (De Steven, 1991b). Cela s'inscrit en partie dans le modèle de succession de tolérance de Connell et Slatyer (1977), puisque les espèces de succession tardive (les arbres) remplacent éventuellement les espèces pionnières (les plantes herbacées). Néanmoins, ces dernières peuvent quand même avoir des effets de compétition sur les arbres. Au contraire, si la survie et la croissance de certaines espèces d'arbres sont fortement atténuées par la végétation herbacée, alors elles s'inscrivent davantage dans le modèle d'inhibition (Connell et Slatyer, 1977 ; De Steven, 1991b).

En analysant les taux de survie et de croissance après cinq ans des arbres plantés dans la végétation et sans protection contre les petits mammifères, nous estimons que les espèces non pionnières et modérément tolérantes à l'ombre (chêne rouge et bouleau jaune) seraient principalement associées au modèle d'inhibition alors que les espèces pionnières, ainsi que l'espèce hautement tolérante à l'ombre (érable à sucre), seraient davantage tolérantes à la végétation herbacée (Chapitre 2). Les conifères quant à eux représentent un degré plus élevé de tolérance car ni leur survie ni leur croissance ne sont diminuées par la végétation herbacée. Des effets de facilitation ont même été détectés sur la survie et la croissance en hauteur du mélèze laricin. La facilitation ne s'observe donc pas uniquement dans les milieux extrêmes ou xériques comme les déserts et les milieux alpins (Holmgren *et al.*, 1997; Brooker *et al.*, 2008; Gómez-Aparicio, 2009). Malgré un milieu mésique, les communautés herbacées auraient agi comme des plantes protectrices (« nurse plants ») pour les plants de mélèze en offrant un milieu plus ombragé et plus humide en surface (Callaway et Walker, 1997; Holmgren *et al.*, 1997; Padilla et Pugnaire, 2006).

Dans le cas de la facilitation par les microorganismes de sol forestier (Chapitre 3), notre étude confirme que les effets sont peu importants lorsque la disponibilité des nutriments d'un site est grande (Jonsson *et al.*, 2001; Smith et Read, 2008; Brooker *et al.*, 2008). Des effets de facilitation ont été observés sur la croissance des espèces d'arbres EM, mais pratiquement aucun effet positif n'a été détecté sur les espèces d'arbres AM. Le taux élevé de phosphore (P) contenu dans le sol agricole de cette expérience est l'une des raisons pouvant expliquer le peu

d'effets positifs engendrés par les microorganismes de sol forestier ajoutés sur les arbres plantés en champ. En effet, la colonisation des racines par les champignons endomycorhiziens (AM) diminue lorsque la disponibilité en P augmente et les champignons endomycorhiziens (AM) sont plus efficaces lorsque le P est limité (Wiseman et Wells, 2005; Smith et Read, 2008). En outre, un faible taux de carbone (C) organique dans le sol agricole peut aussi diminuer les effets positifs ou même être à l'origine d'effets négatifs sur la croissance des jeunes arbres en raison de la demande en C par les champignons mycorhiziens (Johnson *et al.*, 1997; Jones et Smith, 2004; Smith *et al.*, 2009).

Tout comme la relation entre les plantes herbacées et les arbres plantés, celle entre les microorganismes et les arbres peut aussi varier des effets positifs aux effets négatifs. Toutefois, la relation avec les mycorhizes pourrait toujours être perçue comme du mutualisme si on considère que les échanges de coûts et de bénéfices entre l'arbre et le champignon mycorhizien profitent au bout du compte à la valeur adaptative (*fitness*) des deux espèces (Jones et Smith, 2004). Qu'elle soit engendrée par les plantes herbacées ou par les microorganismes, nos expériences confirment que les effets de facilitation varient entre les espèces, au courant du cycle de vie de l'espèce et selon les conditions environnementales.

L'autre grand résultat du chapitre trois est que seulement une espèce typique des forêts tempérées sur les quatre testées a montré des signes de rétroaction négative (« negative feedback ») sur sa croissance, suite à l'ajout de sol forestier recueilli sous des arbres mature de la même espèce. D'une part, cela signifie que les espèces d'arbres des forêts tempérées n'ont pas la même vulnérabilité aux effets possibles de rétroaction négative induits par des ennemis microbiens communs. D'autre part, cela supporte l'idée que l'effet Janzen-Connell ne serait pas aussi dominant en milieu tempéré qu'en milieu tropical (Janzen, 1970; Connell, 1971; Hille Ris Lambers *et al.*, 2002).

4.2 Recherche future et recommandations

Alors que les espèces ayant de larges semences comme les chênes pourraient être ensemencés, les espèces pionnières ayant de petites semences ne semblent pas être de bonnes

candidates pour l'ensemencement en champ. Toutefois, il est possible que nous n'ayons pas utilisé assez de semences pour ces espèces, dont la stratégie de reproduction est de produire de très grandes quantités de semences pour l'établissement de quelques semis. Nous recommandons également de tester l'ensemencement plus tôt au printemps car la température est un facteur important pour la germination de plusieurs espèces (Burton et Bazzaz, 1991). Certaines espèces ont aussi besoin d'un substrat humide pour germer (Godman et Krefting, 1960). L'étude pourrait donc être refaite en ensemençant davantage de semences plus tôt au printemps lorsque le sol est encore humide et elle pourrait être complémentée par une irrigation afin de tester l'hypothèse de l'importance d'un substrat humide pour une bonne germination.

Avec notre dispositif protégeant contre les vertébrés (oiseaux et mammifères), nous n'avons pas détecté de prédation des semences, mais cela ne veut pas dire qu'il n'y en ait pas eu. En milieu tropical, les fourmis peuvent faire autant de prédation sur les semences d'arbres que les vertébrés (Andersen, 1987 ; Woods et Elliott, 2004 ; Garcia-Orth et Martinez-Ramos, 2008). Les fourmis étaient très abondantes sur notre site d'étude et elles ont peut-être été un des facteurs du faible établissement des espèces d'arbres ayant de petites semences. La prédation et la dispersion des semences d'arbres par les espèces invertébrées pourraient donc y être évaluées, d'autant plus que cela n'a pratiquement pas été étudié en milieu tempéré (Hulme, 1998 ; Hulme et Borelli, 1999).

Dans un souci de protection de l'environnement, il importe également de restreindre l'utilisation de matériel non biodégradable comme les paillis ou les protecteurs si les conditions le permettent (par exemple, faible risque de prédation). En effet, ces matériaux nécessitent de retourner sur le site après quelques années pour les retirer, ce qui n'est pas toujours prévu dans les coûts d'aménagement. Bien sûr, les espèces moins susceptibles à la prédation ou à la compétition herbacée comme les conifères pourraient être privilégiés, mais dans une optique de biodiversité et de résilience, on ne devrait pas se limiter à celles-ci. Les plantations devraient être diversifiées et les différentes espèces devraient être dispersées au sein des sites à restaurer afin de réduire la concentration à un seul endroit des effets de la

prédation ou des autres perturbations possibles. D'autres techniques de plantation devraient être testées afin de promouvoir les relations de facilitation. Par exemple, des plantations diversifiées d'espèces à croissance rapide et plus lente pourraient être faites en petits îlots entourés d'arbustes épineux.

Nous avons avancé l'idée que le système racinaire superficiel du mélèze était l'une des raisons expliquant les effets de facilitation par la végétation herbacée (Chapitre 2). Il y aurait possibilité de faire une étude comparant la survie, la croissance aérienne et la croissance racinaire d'espèces de conifères à celles d'espèces feuillues plantées dans la végétation herbacée ou dans un sol à nu. La moitié des arbres pourraient être arrosés afin de voir si l'effet possible de facilitation est influencé par la disponibilité en eau.

Notre étude utilisant des transferts de sol forestier n'a pas démontré de bénéfices assez grands pour justifier d'aller chercher du sol en forêt pour l'ajouter autour d'arbres plantés en champ. Il serait toutefois intéressant de refaire l'expérience sur des sites plus pauvres que celui que nous avons utilisé afin de voir si davantage d'effets de facilitation seraient observés. Cela pourrait être fait dans une optique de restauration d'anciens sites miniers par exemple. En ce sens, une étude menée en Alaska a montré des résultats prometteurs pour la reforestation de terrains miniers abandonnés (Helm et Carling, 1993). Cependant, elle utilisait seulement deux espèces d'arbres (*Populus balsamifera* et *Alnus crispa*) qui font des associations à la fois avec les champignons AM et avec les champignons EM. Les mêmes facteurs que ceux de mon étude pourraient être repris. L'importance des nutriments pourrait être comparée à celle des microorganismes de sol forestier en ajoutant du sol stérilisé ou non, en petite ou en plus grande quantité (ainsi qu'un témoin), sur un site plus pauvre que le sol forestier ajouté. En outre, on pourrait voir si les espèces d'arbres EM tirent plus de bénéfices de transfert de sol forestier que les espèces d'arbres AM sur un site qui devrait contenir peu des deux types de mycorhizes. Je recommande d'utiliser des plants qui auront germé en serre dans un substrat stérilisé ou sinon de mesurer la colonisation mycorhizienne des racines des arbres avant plantation. L'identification des espèces de mycorhizes présentes sur les arbres avant plantation comparée aux espèces présentes quelques mois ou quelques années après

l'ajout de sol forestier ainsi que celles sur les plants du témoin aiderait à comparer les effets de l'abondance de la colonisation mycorhizienne aux effets de la diversité et de la spécificité.

L'étude pourrait aussi être menée dans une optique de changements climatiques et de recherche sur la migration assistée afin de voir si les espèces d'arbres AM qui s'établissent dans la forêt boréale, dominée par les espèces d'arbres EM, seraient avantagées par l'ajout de petites quantités de sol pris dans une forêt dominée par les espèces AM. L'étude pourrait être menée sur un gradient latitudinal de transition de la forêt feuillue à la forêt mixte, jusqu'à la forêt dominée par les conifères. Elle pourrait même être comparée à un gradient altitudinal où les effets devraient être moins perceptibles puisque les spores peuvent s'y disperser par le vent, les animaux et les invertébrés.

Finalement, une grande étude pourrait être entreprise afin de quantifier les effets de compétition, facilitation (ou mutualisme) et les effets pathogènes (hypothèse de Janzen-Connell) en forêt tempérée sur plusieurs espèces d'arbres. Des arbres d'espèces AM et EM pourraient être germés en serre, dans un substrat stérilisé, puis plantés en forêt tempéré à différentes distances d'un individu mature de la même espèce ou d'une autre espèce. Teste et Simard (2008) ont trouvé que les effets de compétition de l'arbre mère sur ses semis s'observaient à moins de 2,5 m et que les effets de facilitation engendrée par la connexion au réseau ectomycorhizien étaient plus importants entre 2,5 et 5 mètres de distance des arbres matures. Cependant, ils ne sont pas attardés aux effets possibles d'ennemis communs (hypothèse de Janzen-Connell) et ils ont fait cette étude sur une seule espèce (sapin Douglas). S'il découle de ces études que je propose que l'effet Janzen-Connell est en effet peu commun en forêt tempérée et que les transferts de sol sont utiles sur des sites pauvres, alors les sols pourront être pris dans une forêt dominée par des espèces d'arbres de la même association mycorhizienne que les arbres plantés même si des individus conspécifiques se trouvent dans cette forêt.

Contrairement aux plantations ayant un objectif de productivité forestière, les plantations d'arbres utilisées pour la restauration des terres agricoles abandonnées ne visent pas

nécessairement une croissance rapide. Elles ont comme objectif de créer à long terme un couvert d'arbres diversifié qui permettra aux espèces typiques des forêts de coloniser et de fréquenter ces nouveaux milieux. Un écosystème est considéré comme restauré lorsqu'il contient suffisamment de ressources biotiques et abiotiques pour continuer son développement sans assistance (Society for Ecological Restoration International Science & Policy Working Group, 2004). Les techniques de restauration devraient donc favoriser davantage la survie des arbres que leur croissance rapide. Ainsi, plusieurs espèces d'arbres peuvent être plantées directement dans la végétation même si cela ralentit leur croissance tant que leur survie n'y est pas trop atténuée. Par contre, la protection contre la prédation peut s'avérer nécessaire dans certains environnements. La plantation d'arbres de plus gros calibres pourraient aussi augmenter leur survie face aux prédateurs.

Cette thèse a montré que les taux de germination, survie et croissance varient en fonction des caractéristiques des espèces d'arbres ainsi que de l'environnement entourant les arbres. Malgré leur apparence homogène, les micro-conditions environnementales des terres agricoles abandonnées et des friches herbacées sont variables et elles influencent les interactions biotiques. À l'image de l'agriculture de précision, qui tient compte de la variabilité à l'intérieur d'un champ (Brisco *et al.*, 1998), la restauration forestière devrait donc se faire à une échelle plus fine que l'ensemble de la superficie du site à restaurer. En outre, il ne faut pas se limiter à établir que les espèces d'arbres les plus faciles à restaurer, mais trouver des nouvelles approches simples et peu coûteuses afin de faciliter la restauration du plus grand nombre d'espèce. Cette thèse constitue une contribution à l'élaboration de méthodes efficaces et écologiquement acceptables afin de renverser la perte de couvert forestier.

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